UNIVERSITY OF LONDON THESIS

Degree PhD Year 2007 Name of Author LEIGHTON, Jane

Automatic and intentional imitation: Experiments with typically developing adults and adults with autism spectrum disorders

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A thesis submitted to the

Faculty of Science

of the University of London

for the degree of Doctor of Philosophy

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Abstract

There are four main theories addressing the core mechanisms of imitation. Two of these theories suggest that imitation is mediated by a special-purpose mechanism and two suggest that it is mediated by general learning and motor control mechanisms. The main purpose of this thesis is to examine whether the question of how we imitate is best answered by specialist or generalist theories.

In order to do this, experiments have been carried out using both intentional and automatic imitation paradigms. These paradigms have been used to examine imitation skills both in typically developing individuals and individuals with autism spectrum disorder (ASD).

The first empirical chapter examines the role of goals in imitation. Specialist theories claim that goals play an integral role in explaining how we imitate. Some of the best evidence in support of this view is provided by error patterns generated in the pen-and-cups task. However, the results from variants of the pen-and-cups task, presented in this chapter, are more consistent with the idea that general processes, rather than goals, guide imitative behaviour.

Chapters 3 and 4 examine imitative abilities in ASD using intentional and automatic imitation paradigms in order to ascertain whether there is an imitation specific impairment in ASD. Such an impairment would appear to be consistent with specialist theories of imitation. However, the findings from these chapters imply that the basic mechanism mediating imitation is not impaired in ASD, and that poor performance on complex intentional imitation tasks in ASD may be due to more generalised deficits, not specific to imitation.

The final empirical chapter addresses effector specificity in imitation and whether this phenomenon can distinguish between specialist and generalist accounts of imitation. Using an automatic imitation paradigm, partial effector specificity is demonstrated, which is consistent with claims made by generalist theories.

The first three empirical chapters therefore challenge some of the evidence that has been put forward to support specialist theories, and the final empirical chapter provides some specific support for generalist theories. Thus, the findings reported in this thesis are consistent with the hypothesis that imitation is mediated by general processes rather than by a special-purpose mechanism.

Acknowledgements

There are many people who have given me a great deal of help over the last three years. I am grateful to these individuals for their technical and intellectual support and also for making these years so enjoyable. These include the members of the Heyes lab, past and present; all UCL Psychology Department staff and students; and the London University Swimming Team.

Special thanks must go to Tony Charman, for all the extra help and advice and Geoff Bird, to whom I owe a great deal. Thanks Geoff, for always being on hand for encouragement and guidance, and for often going beyond the call of duty.

I am especially grateful to my supervisor, Celia Heyes, for all her hard work. I have learned a great deal from Celia, and her time, effort and wisdom have been invaluable to me. I'd like to thank her for her patience, kindness, numerous words of encouragement and also for giving me this opportunity. Thanks for everything, Celia.

Thanks must also go to the Medical Research Council, who, through awarding me a studentship, made it financially possible for me to complete this PhD.

Finally, I'd like to say a special thank you to my parents for their endless support, for always being there for me, and for providing me with so many opportunities. I can never thank you enough but I hope you have some idea of how much I appreciate everything you've done for me.

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Chapter 1: Introduction

1.1 Imitation

An executed action is said to match an observed action when it is visually similar from a third party perspective. Imitation is the term used to refer to behaviour of this type, where one performs an action which matches an observed action and which is causally related to having observed that action (Dautenhahn & Nehaniv, 2002).

Imitation is regarded as one of the most important means whereby skills and behaviour are transferred between agents. It is thought to play an important role in language acquisition, skill learning, socialization, and enculturation (e.g. Byrne & Russon, 1998; Meltzoff & Gopnik, 1993; Trevarthen, 1984; 1994). A growing body of evidence suggests that imitation also plays a significant role in our understanding of both ourselves and others (e.g. Meltzoff, 2002; Tomasello, Kruger & Ratner, 1993). Imitation is, therefore, an important process during early development and throughout adulthood.

Imitation is investigated by many researchers with different purposes. For example, comparative psychologists are interested in whether animals are capable of imitation (e.g. Custance, Whiten & Bard, 1995; Voelkl & Huber, 2000). Those investigating 'observational learning' address whether and how observing another performing an action can accelerate learning of that action (e.g. Bird & Heyes, 2005; Kelly & Burton, 2001). Social psychologists are concerned with relationships between imitation and other sociocognitive functions such as empathy (e.g. Chartrand & Bargh, 1999). Cognitive neuroscientists are preoccupied with identifying the neural mechanisms of imitation (e.g. Iacoboni, 2005). Developmental psychologists are interested in the age

at which children begin to imitate (e.g. Meltzoff & Moore, 1997) and whether imitation can reveal mental state understanding capabilities in infants (e.g. Gergely, Bekkering, & Kiraly, 2002).

Given the importance of imitative behaviour, a number of theories have been put forward to explain the phenomenon. Investigations into imitation tend to focus on two issues; *how* we are able to imitate and *what* we imitate. The purpose of this thesis is to address the question of *how* we imitate. The first chapter begins in this section by discussing the main explanatory challenge faced by research on imitation. Section 1.2 will outline four theories that attempt to address this issue and section 1.3 will examine evidence which has been proposed to support the various theories. Finally, section 1.4 will summarise the previous research and hypotheses under investigation in this thesis, along with ways in which they will be tested in the subsequent empirical chapters.

Although, intuitively, copying another person seems a simple task, understanding how we achieve this raises an important problem, known as the correspondence problem (Alissandrakis, Nehaniv, & Dautenhahn, 2002; Brass & Heyes, 2005; Nehaniv & Dautenhahn, 2001). Many processes are needed for effective imitation, such as vision, motor control and working memory. However, the correspondence problem is what distinguishes imitation from other types of perception and action tasks. When we observe another person moving we do not see the muscle activation underlying their movement but rather the external consequences of that activation. This visual representation of an action must be translated into the motor commands needed to carry out a matching action. Visual and motor representations would appear to be in incommensurable codes. How, therefore, does the observer's motor system 'know' which muscle activations will lead to the observed movement?

This problem is particularly difficult for perceptually opaque or 'invisible' actions (Heyes & Ray, 2000; Piaget, 1962) where the visual feedback generated when executing the action oneself differs from the visual feedback generated when observing another individual executing the action. In these cases, simple perceptual matching cannot be used to produce imitative movements. The correspondence problem is, therefore, particularly important for whole body movements and facial gestures where the observer receives minimal visual feedback when executing the action.

Consider the following example: a swimming teacher demonstrates butterfly technique to a novice swimmer. To imitate the teacher successfully, the swimmer is required to perform an action that matches from a third party perspective; however, the two actions will not match from the novice's perspective. The swimmer will perceive the teacher's actions as a whole body movement where the arms, from an outstretched position in front of the body, move under the body with the elbows kept high. When the hands reach the hips, the arms are swung forward, above the surface of the water, so that they reach the front again. In contrast, the swimmer's own actions will be perceived as a movement of their arms from an outstretched position in front of them to an unseen position under their body and then to the unseen arm recovery above the water.

Thus, an important challenge for theories of imitation is to explain *how* observation of action facilitates production of matching movements. This chapter reviews four theories of imitation which approach this problem in different ways.

1.2 Theories of imitation

Theories that address imitation fall into two categories: specialist and generalist theories (Brass & Heyes, 2005). Specialist theories propose that imitation is mediated by a special-purpose mechanism whereas generalist theories suggest that it is mediated by task-general learning and motor control mechanisms. Special-purpose mechanisms, or 'cognitive modules', are hypothesised to explain why and how we develop competencies in specific domains in ways that could not be predicted on the basis of environmental inputs and general learning mechanisms alone. In direct contrast to this view, generalist theories suppose that environmental inputs and general learning are sufficient to explain the development of a particular competency. Two specialist theories, the active intermodal mapping model (AIM, e.g. Meltzoff & Moore, 1997) and the theory of goal-directed imitation (GOADI, Bekkering, Wohlschläger & Gattis, 2000; Wohlschläger & Bekkering 2002; Wohlschläger, Gattis & Bekkering, 2003) propose mechanisms specific to imitation that mediate imitative behaviour. There are two complementary generalist theories: ideomotor theory (IM, e.g. Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Prinz, 1997; 2002), which subsumes imitation within a general account of motor control, and the associative sequence learning model (ASL, Brass & Heyes, 2005; Heyes, 2001; Heyes, 2003; Heyes & Ray, 2000), which claims that the capacity to imitate is a product of task- and species-general processes of associative learning.

Both specialist and generalist theories propose alternative solutions for solving the correspondence problem. Four theories of imitation and their explanations for how we imitate are described below.

1.2.1 Active intermodal mapping (AIM)

The most prominent specialist theory is Meltzoff & Moore's AIM model of imitation (e.g. Meltzoff & Moore, 1997). This theory was developed in order to explain the imitation of facial gestures in newborn infants, sometimes as young as 32 hours (Meltzoff & Moore, 1977; 1983; 1989; 1997). Meltzoff & Moore (1977; 1997) suggest that this phenomenon provides the best evidence in favour of a special-purpose mechanism for imitation because general learning mechanisms and environmental input cannot account for a skill present so shortly after birth. The special-purpose mechanism proposed is a supramodal representation system which allows a visual representation of an action to be matched with the motor representation of that action.

The AIM model outlines a number of stages said to account for neonatal imitation: The infant's first response to seeing a modelled action is activation of their corresponding body part. Referred to as 'organ identification', this is the process by which infants can identify their own and others' body parts. Meltzoff & Moore argue that an ability to identify corresponding body parts renders self and other in commensurate terms, as movements of body parts such as tongues, lips and hands. According to this view, organs, or body parts, are cross-modal units of analysis.

The second stage in generating an imitative response is the movement component. Meltzoff & Moore (1997) suggest that newborn infants do not know which muscle movements will result in a particular bodily state. They propose that 'body babbling' enables infants to learn the relationships between muscle movements and the bodily states which result. Body babbling may occur in utero and results in learned relationships between movements and bodily states. After such experience-dependent learning, the infant will have the ability to produce muscle movements leading to

specified bodily states. Bodily states are referred to by Meltzoff & Moore as 'organ-relations' and are said to represent configural relations between organs, for example tongue-to-lips. Organ relations constitute the cross-modal metric of equivalence necessary to solve the correspondence problem, and thus explain *how* imitation is done. According to the authors, "organ relations render commensurate the seen but unfelt act of the adult and the felt but unseen act of the infant" (p185, Meltzoff & Moore, 1997).

Organ relations provide a nonverbal coding of human action that is not at the level of motor commands but at the level of the *goal of the act.* Meltzoff and Moore (1997), therefore, claim that imitation is goal-directed. They state that imitative responses are not motor units akin to reflexes that are simply released by the appropriate input. Rather, imitation is a goal-directed response, the aim of which is 'matching the target'.

The AIM model, therefore, offers an explanation for neonatal imitation and is also said to form the basis for adult imitative competency (Meltzoff & Moore, 1997). However, the model is currently underspecified in a number of ways. First, it is not clear how organ relations become cross-modal units, and therefore, able to solve the correspondence problem. The hypothesis does not specify a code in which organ relations are represented; aside from denying that these codes are modality specific, little information is given, therefore, it is not clear how this content is encoded. Furthermore, it is not clear how learning via body babbling results in the formation of these cross-modal units of action.

Second, there is an ambiguity within the theory concerning what constitutes a goal. In the original specification of the theory, it is stated that actions are coded in terms of

organ relation end-states. Therefore, goals are observable outcomes of movement; for example a fist may be the outcome of a hand closing movement. However, more recently, it has been implied that these goals are higher level cognitive processes relying on the understanding of another's intentions (Meltzoff, 1995; 2007). Under this view, goals are understood to be mental states that the imitator ascribes to the model, and as a result, imitation relies on inferring the intentions of others. Therefore, it is unclear exactly what is meant when Meltzoff and Moore state that actions are represented at the level of the goal of the act (Meltzoff & Moore, 1977).

Goals and their relevance to imitation are also highlighted by the second specialist theory addressed in this thesis.

1.2.2 Theory of goal-directed action (GOADI)

The second specialist theory addressed in this thesis is the theory of goal-directed action (GOADI). GOADI is based on findings from developmental research where young children often imitate the ends of a movement while ignoring the means (Wohlschläger & Bekkering 2002; Bekkering et al., 2000; Wohlschläger et al., 2003). For example, when copying an adult drinking from a cup, the child will concentrate on moving the cup to their lips (ends) without considering the way in which the ends are achieved (means), for example, the way in which the cup is manipulated.

GOADI consists of a number of postulates:

> "i) *Decomposition.* The perceived act is cognitively decomposed into separate aspects. ii) *Selection of goal aspects.* Owing to capacity limitations, only a few goal aspects are selected. iii) *Hierarchical organization.* The selected goal aspects are hierarchically ordered. The hierarchy of goals follows the

functionality of actions. Ends, if present (e.g. objects and treatments of the latter) are more important than means (e.g. effectors and movement paths). iv) *Ideomotor principle*. The selected goals elicit the motor programme with which they are most strongly associated. These motor programmes do not necessarily lead to matching movements, although they might do so in many everyday cases. v) *General validity*. There is no essential difference in imitation behaviour between children, adults and animals. Differences in accuracy are due to differences in working memory."

(Wohlschläger et al., 2003, p503).

Actions are, therefore, broken down into a number of sub-goals. Some goals take priority over others if processing demands are high. This results in some aspects of a movement being accurately copied at the expense of other, less important aspects.

GOADI constitutes a specialist theory of imitation for the following reasons: The theory suggests that the goal selection processes mediating imitation are special; that is, it suggests that these processes are distinct from those mediating performance of other perceptual and motor tasks. GOADI implies that decomposition, selection of goal aspects and hierarchical organisation are imitation-specific processes necessary to explain how an observed action is translated into motor output. This claim about the distinctiveness of the goal selection processes mediating imitation is implicit in GOADI. It is presented as a theory of imitation, goal selection processes are key features of the theory, and unlike the ideomotor principle they are not said to characterise performance in other non-imitative tasks. Furthermore, the design of some of the experiments conducted by the authors of GOADI, indicate that the theory is intended to apply to imitative and not non-imitative action (e.g. Wohlschläger et al.,

2003). Finally, GOADI is explicitly presented as a theory designed to explain how we imitate. If these processes apply to other non-imitative tasks, then it is not clear how GOADI would constitute a theory of imitation.

In order to solve the correspondence problem, GOADI assumes that the mirror neuron system "transforms movements perceived from others into the actor's own possible action goals". An action, therefore, becomes represented in terms of its goal. Selected goals then elicit the motor programme with which they are most strongly associated (Bekkering, 2002). Therefore, this theory proposes that goals are necessary as an intermediate stage in order to translate visual representations into motor representations (Bekkering & Wohlschläger, 2002). However, like AIM, GOADI is unclear about the exact meaning of the term goal. Some of the authors of GOADI suggest that goals are observable action outcomes (Wohlschläger et al., 2003), whereas others suppose that goals are inferences about the model's intentions (Gattis, Bekkering & Wohlschläger, 2002).

Both AIM and GOADI highlight the intrinsic role of goals in imitation and claim that imitation is mediated by a special-purpose mechanism. The following sections provide an alternative view by describing two generalist theories.

1.2.3 Ideomotor theory (IM)

IM proposes that imitation is mediated by general processes (e.g. Brass et al., 2001; Brass et al., 2000; Prinz, 1997; 2002; Hommel, Müsseler, Aschersleben & Prinz, 2001). The theory is based on Greenwald's (1970a; 1970b) extension of the ideomotor theory of action (James, 1890). James argued that, "Every representation of a movement awakens in some degree the actual movement which is its object" (James,

1890, p. 1134); suggesting a model of action control in which the idea, or mental representation, of a movement is sufficient to cause its execution without any further need for volition. Greenwald extended this concept to include two central claims; that actions are mentally represented in terms of their perceptual effects, and that these effect representations are used to control action production (Greenwald, 1970a; 1970b). Prinz (1997) argued that IM provides a useful framework to understand imitation because it demonstrates how action perception may prompt the production of a matching movement.

IM specifies that perception and action share a common representational framework, and therefore does not need to specify a mechanism for translation of motor and perceptual representations. This approach apparently eschews the correspondence problem. Under IM, actions are represented in terms of their sensory consequences, enabling information received through the senses to be matched to sensory consequences contained in action representations. Action representations can, therefore, be used to control action production by comparing expected sensory feedback with actual sensory feedback (Wolpert & Kawato, 1998). A perceptual stimulus activates the action representation with which it exhibits the most ideomotor similarity. Ideomotor similarity refers to the degree to which features of a stimulus correspond to sensory features produced by particular actions. As actions are represented in terms of their perceptual effects, perceptual input from the model can be compared directly with the observer's action representation.

This process can be illustrated through imitation of a hand opening movement. Visual information received when a hand opening action is observed will activate any action representation with which it shares some degree of ideomotor similarity. The action

representation which exhibits the greatest degree of similarity will be activated most strongly, and in the majority of cases this will be the 'hand opening' action representation. When an action representation is activated, the individual will perform the action without the need for any further volition unless the action is actively inhibited. IM, therefore, does not suppose any special-purpose mechanisms to be involved in imitation. It assumes that the ability to imitate is simply due to the general organisation of motor control.

While IM does offer some explanation as to how we imitate, it does not explain how we are able to copy perceptually opaque actions because the sensory consequences of executing an opaque action will not be similar to the sensory features of observing that action. However, if IM is combined with the hypothesis that actions acquire their common codes through associative learning (Elsner & Hommel, 2001; 2004), it may be able to explain imitation of perceptually opaque actions. The idea that actions and their sensory consequences become linked through associative learning forms the basis for the second generalist theory addressed in this thesis and will be elaborated further in the following section.

1.2.4 Associative sequence learning (ASL)

The associative sequence learning model of imitation (ASL, Brass & Heyes, 2005; Heyes, 2001; Heyes, 2003; Heyes & Ray, 2000) also proposes that imitation is guided by general-purpose mechanisms. The theory suggests that the ability to imitate develops through learning bidirectional links between visual and motor representations of actions, 'matching vertical associations'. These associations can form whenever an individual experiences concurrent observation and execution of the same movement (contiguity). Furthermore, in line with contemporary theories of associative learning

(e.g. Rescorla & Wagner, 1972; Hall, 1994), ASL assumes that in addition to contiguity, the formation of vertical associations relies on contingency between observed and executed movements.

Opportunities to associate visual and motor representations of the same actions are abundant during development. For perceptually transparent actions, such as hand and arm actions, the opportunities for associative learning can be provided through self observation. For example, observation of oneself performing a hand opening action results in the co-activation of the perceptual and motor representations of hand opening. This co-activation will result in the perceptual and motor representations becoming associated. For perceptually opaque actions, such as face movements, the visual input received upon execution differs from that received upon observation of another performing that action. However, there remain many types of experience which provide opportunities for relevant associative learning even for opaque actions.

First, adults frequently imitate infants (Field, Guy & Umbel, 1985; Papousek & Papousek, 1989). Second, within our environment there are many reflective surfaces and mirrors, allowing direct observation of action. Third, events in the environment may lead to similar reactions in oneself and others at the same time. For example, if something unpleasant is present in the environment a number of individuals may react with an expression of disgust. One will, therefore, observe a disgusted facial expression at the same time as producing such an expression. The examples above all provide opportunities for concurrent experience of 'seeing' and 'doing', and therefore allow matching vertical associations between motor and visual representations to be formed. Finally, vertical associations can be established indirectly through common associations with other representations of action. For example, verbal representations

of action may mediate visual and motor associations; one may often hear the word smile when smiling oneself and also when observing someone else smile. Through common associations with the word smile, associations may form between the visual and motor representations of a smile (e.g. Rescorla & Wagner, 1972).

The ASL model proposes that novel action sequences can be imitated through additional processes which are not unique to imitation (Heyes & Ray, 2000). This novel imitation, or imitation learning, is possible because an observed action can be broken down into constituent familiar elements or movement primitives arranged in a sequence. The sequence of these primitives is learnt through processes which operate whenever an individual learns a sequence of visual stimuli (forming 'horizontal' associations). When this visual sequence is learned, it is possible to imitate this novel sequence through previously learned vertical associations between visual and motor representations of the familiar movement primitives.

The ASL model, therefore, provides an account of how visual and motor representations may be associated, thereby explaining *how* imitation is possible. IM and ASL are largely compatible as both theories describe imitation as a product of general processes. Both theories are also compatible with a range of recent findings using automatic imitation paradigms (see section 1.3.4.1). As highlighted above, the main difference between them, being that in contrast with ASL, IM does not explain how sensorimotor links or common codes are formed. ASL, therefore, takes IM one stage further by providing an explanation of how the correspondence problem is solved both for transparent actions, and also for opaque actions.

1.3 Evidence distinguishing the theories

It may be possible to distinguish between the theories highlighted in this section by examining a range of evidence. Specialist and generalist theories make different claims with respect to the properties of imitation (Fodor, 1983).

First, specialist theories assume that environmental input and general learning mechanisms cannot sufficiently explain how we imitate. In direct contrast to this view, generalist theories suggest that environmental input and general learning mechanisms are sufficient to explain imitation. Therefore, generalist theories highlight the role of learning in imitation whereas specialist theories do not.

Although innateness is not necessarily a requirement of a special-purpose mechanism - a module could quite plausibly develop over ontogeny without being pre-specified (Karmiloff-Smith, 1992) - discussion of modules in the cognitive development literature commonly assumes that modularity and innateness are directly linked (e.g. Fodor, 1983). Therefore, if imitation is demonstrated to be innate, this is more consistent with specialist claims than with generalist claims which would undoubtedly deny an innate imitation mechanism.

Second, special-purpose mechanisms are assumed to be domain specific, that is, they exclusively handle a specific class of stimuli (Fodor, 1983). In the case of imitation, it is likely that this will be human action stimuli. On the contrary, since generalist theories deny any special imitation mechanism, they would not expect strict domain specificity in imitation.

Third, at a neurological level, special mechanisms are typically seen as dedicated brain areas that subserve specific cognitive functions. Consequently, if a special-purpose mechanism for imitation exists, it should be possible to identify dedicated neural areas that mediate imitation-specifically. Furthermore, imitation and brain regions dedicated to imitation should be susceptible to selective impairment, that is, deficits in imitation that are not associated with more generalised deficits. Alternatively, generalist theories would not necessarily expect to find dedicated brain areas that subserve imitation or selective imitation impairments.

The following sections will examine a range of evidence that may allow distinctions to be drawn between specialist and generalist theories of imitation. In section 1.3.1, the neural mechanisms of imitation will be explored. Sections 1.3.2 and 1.3.3 describe studies on development, both typical and atypical. Finally, section 1.3.4 examines imitation in healthy adults by describing studies investigating automatic imitation (1.3.4.1), the effect of animacy on imitation (1.3.4.2) and training and expertise (1.3.4.3).

1.3.1 Neural mechanisms of imitation

A number of studies using electrophysiological and imaging techniques have identified cortical areas that are active both during observation and execution of a particular action. Cells of this kind, named 'mirror neurons', were first discovered in the premotor and parietal cortices of macaques, and fire both when the monkey observes and executes an action (di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992; Ferrari, Maiolini, Addessi, Fogassi & Visalberghi, 2005; Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Keysers, Kohler, Umilta,

Nanetti, Fogassi & Gallese, 2003; Kohler, Umilta, Fogassi, Gallese & Rizzolatti, 2002; Rizzolatti, Fadiga, Gallese & Fogassi, 1996; Umilta, Kohler, Gallese, Fogassi, Fadiga, Keysers & Rizzolatti, 2001).

Increasing evidence suggests that neurons or neural areas with the same properties are present in the human brain. These areas have been demonstrated to be active both during execution and during passive observation of action and are thought to be homologous to those areas demonstrating mirror properties in the monkey brain. For example, functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies have found premotor and parietal activation when observing hands grasping objects (Grezes, Armony, Rowe & Passingham, 2003; Hamzei, Dettmers, Glauche, Weiller & Buchel, 2003), hands manipulating objects (Chaminade, Meltzoff & Decety, 2002; Decety, Chaminade, Grezes, & Meltzoff, 2002; Montgomery, Isenberg & Haxby, 2007), pantomimes of hand actions with objects (Decety, Grezes, Costes, Perani, Jeannerod, Procyk, Grassi & Fazio, 1997; Grezes, Costes & Decety, 1999; Grezes, Costes & Decety, 1998), and speech-related and biting actions (Buccino, Vogt, Ritzl, Fink, Zilles, Freund & Rizzolatti, 2004). Electroencephalography (EEG) and magnetoencephalography (MEG) methods also provide converging evidence that motor processes operate when observing hand actions (Babiloni, Babiloni, Carducci Cocozza, Del Percio, Moretti, Rossini, 2002; Cochin, Barthelemy, Roux & Martineu, 1999; Hari, Forss, Avikainen, Kirveskari, Salenius, & Rizzolatti, 1998; Muthukumaraswamy & Johnson, 2004; Nishitani & Hari, 2000), facial expressions (Dapretto, Davies, Pfeifer, Scott, Sigman, Bookheimer & Iacoboni, 2006; Nishitani & Hari, 2002) and whole body movements (Cochin, Barthelemy, Lejeune, Roux & Martineau, 1998).

A large body of evidence, therefore, suggests that observation of action leads to specific activation of motor-related neural populations. Activation of this kind may constitute the neural basis for imitation. Various neural areas, thought to be part of the human mirror system, have been demonstrated to be active during imitation. These include the inferior frontal gyrus (pars opercularis and pars triangularis), the dorsal and ventral premotor cortex, the inferior parietal cortex, the superior parietal lobule and the posterior superior temporal sulcus (Iacoboni, Woods, Brass, Bekkering, Mazziotta & Rizzolatti, 1999; Iacoboni, Koski, Brass, Bekkering, Woods, & Dubeau, Mazziotta & Rizzolatti, 2001; Koski, Wohlschläger, Bekkering, Woods, Dubeau, Mazziotta & Iacoboni, 2002; Buccino et al., 2004, Grezes et al., 2003).

The human mirror neuron system is, therefore, a candidate neural circuit specifically 'for' imitation, which appears to be consistent with a specialist view of imitation. However, the role of some of the areas highlighted above is still controversial and most studies have failed to find areas that are reliably active during imitation but not during passive observation of action. Since it is expected that special-purpose mechanisms are implemented in distinct cortical areas, failure to identify areas that are active during imitation but not passive observation, is not consistent with a specialist view. However, at the present time only tentative conclusions may be drawn from the neuroscience literature. Neuroimaging techniques are not yet sophisticated enough to identify the particular cells active at any particular time. Therefore, there may be neuronal populations specifically active during imitation but our techniques are not yet sensitive enough to detect them. Thus, it is not yet clear whether investigations into the neural mechanisms can provide conclusive evidence in favour of either generalist or specialist theories.

1.3.2 Typical development

1.3.2.1 Neonatal imitation

Some specific support for each of the specialist theories has been provided by studies with infants and older children. The most well-established evidence in support of AIM is the finding that newborn infants can imitate simple facial movements. In 1977, Meltzoff and Moore reported that infants between 12 and 21 days old were more likely to protrude their tongue if they observed a caregiver protruding their tongue rather than opening their mouth. Conversely they were more likely to open their mouth if they observed mouth opening than if they observed tongue protrusion. The authors also reported similar imitative behaviour in newborn infants as young as 32 hours old (Meltzoff & Moore, 1983; 1989). Several other studies have provided evidence of neonatal imitation of a range of actions including mouth opening, hand gestures, head movements, eye blinking, cheek and brow movements and facial expressions (Heinman, Nelson & Schaller, 1989; Kaitz, Meschulach-Safarty, Aurbach & Eidelman, 1988, Reissland, 1988; Vinter, 1986; Kugiumutzakis, 1985; Field et al., 1985; Field, Woodson, Greenberg & Cohen, 1982).

These findings support the idea that imitation is innate, which is consistent with a specialist view of imitation but not with a generalist view. In particular, ASL, which assumes that imitation is a product of sensorimotor associative learning, could not account for imitation of a range of movements in infants too young to have formed sensorimotor associations. Therefore, the most plausible way to account for the broad imitative competence in neonates would be to suppose that a special-purpose mechanism mediates imitation.

However, despite the number of studies claiming to demonstrate neonatal imitation, the effect has not always been replicated. In a meta-analysis of the previous data, Anisfeld (1991; 1996) found that the only gesture for which there is reliable evidence of imitation is tongue protrusion. He argued that in the majority of previous studies, authors have looked for two-way interactions of observed and executed action type, where tongue protrusion was one of the actions. Therefore, any significant effects could be driven by an effect on only one action type; in this case, tongue protrusion. Furthermore, some studies have suggested that rather than representing an imitative response, tongue protrusion may rather be mediated by an arousal process (Ullstadius, 1998; Jones, 1996; 2006). The arousal hypothesis is supported by experiments showing that the frequency of infants' tongue protrusion is elevated, not only after observation of tongue protrusion, but after a comparable period of exposure to flashing lights or lively music (Jones, 1996; 2006).

While findings from studies with neonates have often been cited as supporting nativist and specialist theories, in particular AIM, the problems highlighted above imply that strong conclusions cannot be drawn. Consequently, these studies do not provide conclusive evidence in support of specialist theories. However, studies with older children have provided some specific support for the theory of goal-directed imitation.

1.3.2.2 Imitation in children

Evidence for the importance of goals in guiding imitative behaviour comes from an early finding by Head (1920; 1926), who demonstrated an interesting pattern of errors during hand-to-ear imitation tasks. In the hand-to-ear task, a child faces an adult as, on each trial, the adult touches his left or right ear with his left or right hand (four trial types). From three years of age, children who were either instructed to mirror imitate

these actions (e.g. to copy movements of the model's right hand with their own, spatially compatible, left hand; Bekkering et al., 2000, Gleissner, Meltzoff & Bekkering 2000, Gordon 1923, Wapner & Cirillo 1968), or allowed to imitate spontaneously (Wohlschläger et al., 2003), made an elevated number of errors when a contralateral movement was required. For example, if the adult touched his left ear with his right hand, the child touched her right ear, which is correct, but performed this action using her right hand in an ipsilateral movement path, rather than her left hand in a contralateral movement path. Thus, children imitate object selection - choice of an ear to touch - more reliably than they imitate selection of an effector and movement path, which causes them to make an ipsilateral movement when a contralateral movement is required. These 'contralateral-to-ipsilateral' errors were originally interpreted to be due to neurological immaturity resulting in inability to perform actions crossing the body's midline (Kephart, 1971). This 'lateral bifurcation' hypothesis was challenged by a number of findings such as similar error patterns in much older children (Schofield, 1976) and even in adults in a speeded version of the task (Wohlschläger et al., 2003). Furthermore, Bekkering et al. (2000) showed that when children were asked to copy a model who touched both ears, using a crossed hand movement, fewer contralateral-to-ipsilateral errors were made, indicating that children do not have difficulty performing movements which cross the body's midline.

Bekkering, Wohlschläger and colleagues interpreted errors on contralateral trials as evidence that imitation is goal-directed. They explained their findings in terms of decomposition of the action into sub-goals which are then hierarchically organised. Within this hierarchy, ends take priority over the means. Therefore, the ear, or end point, is the dominant goal and the effector and movement path are subordinate goals. When processing demands are high, the most important goal, ear selection, is

preserved resulting in errors in effector and movement path. However, when participants are required to touch both ears and use both hands, neither hand nor ear selection are necessary, and the number of competing goals is reduced. In this situation, the crossing of the hands becomes a more dominant goal resulting in fewer contralateral-to-ipsilateral errors in that condition.

Variations of the original hand-to-ear experiments described above have provided further evidence for GOADI by again showing that children more accurately reproduce the ends of an action than the means (Bekkering et al., 2000). In the dots task, the child faced the model/experimenter across a table and was asked to copy the model's movements. On each trial, the model touched the table at a location on her left or her right side, using her left or her right hand. The location was marked by a dot, which was fixed to the table. As predicted by GOADI, three-year-old children made more errors when a contralateral movement was required. On these trials, children used an ipsilateral movement to reach the correct goal, thus using the incorrect hand and movement.

In a follow-up experiment where children were required to touch a location on the table when there were no dots present, these contralateral-to-ipsilateral errors were significantly reduced. According to GOADI, objects take precedence as dominant goals. In the absence of objects in the no-dots condition, other sub-goals, such as effector and movement type, take precedence (Bekkering et al., 2000).

Additional variations of the hand-and-ear task appear to have been designed to show that goal processing of the type postulated by GOADI is specific to imitation tasks. In a non-imitative version of the task, when children were shown photographs of the

stimulus movements and asked to select matching photographs, rather than to imitate, they do not make a disproportionate number of contralateral-to-ipsilateral errors (Wohlschläger et al., 2003). This suggests that the goal selection processes described by GOADI are imitation-specific processes.

Finally, in line with GOADI's final postulate, that there is no difference between imitation in adults and children, similar error patterns have been reported in adults. In a speeded version of the dots task, where participants were required to imitate contralateral and ipsilateral finger movements, more contralateral-to-ipsilateral errors were made when the movements were directed to dots than when they terminated at unmarked locations (Wohlschläger & Bekkering 2002).

One task that was designed to specifically test GOADI in adults is the pen-and-cups task. The pen-and-cups task allows three features of action to be manipulated independently: object selection, effector selection and grip selection. On each trial in this speeded response procedure, the participant sees a model move a centrally located pen into one of two coloured cups (object), using his right or his left hand (effector), while grasping the pen with his thumb pointing up or down (grip). Both when they are required to mirror imitate and when they are required to transpose (e.g. right hand movements are copied with the spatially incompatible right hand), adults make fewer cup errors than hand errors and fewer hand errors than grip errors (Avikainen, Wohlschläger, Liuhanen, Hanninen, & Hari, 2003; Wohlschläger & Bekkering, 2002). Consistent with GOADI, this cup<hand<grip error pattern implies that, when processing resources are limited, imitation of object selection takes priority over imitation of effector selection, which, in turn, takes priority over imitation of the details of response topography.

GOADI implies that the goal selection processes that guide performance on the tasks described above are imitation-specific processes. Therefore, the foregoing group of studies apparently provide evidence in support of GOADI as well as more general support for specialist theories. However, generalist theories of imitation offer an alternative explanation for the findings described above. Generalist models suggest that there are no imitation-specific processes, and therefore, that the error patterns seen in tasks such as the pen-and-cups task may be a result of task-general mechanisms such as perceptual and attentional processes, rather than of imitation-specific processes of goal selection. For example, in the pen-and-cups task, in all implementations of the task described above, the cups, but not the hands or the grips, were of different colours. Thus, the cups were more readily discriminable than the hands or the grips. As a result, participants may have made fewer cup errors than hand or grip errors because it was easier for them to determine which of the cups had been selected on any given trial. Similarly, previous studies may have found more grip than cup or hand errors because, in all versions of the task used to date, the two grips were applied at approximately the same spatial location, and only one of them was present in the stimulus display at any given time. In contrast, the model's two cups and two hands were simultaneously present at distinct spatial locations. Therefore, the relatively high incidence of grip errors may have been due to difficulty in perceiving which of the grips had been selected in each trial. Therefore, general perceptual processes, rather than imitation specific goal selection processes, could account for the error patterns seen in the pen-and-cups task. If this is the case, then these error patterns may not be able to provide support for specialist goal directed theories.

Some evidence consistent with this idea has recently been provided by Bird, Brindley, Leighton & Heyes (2007). However, further investigation of this 'general process

account' is necessary to ascertain whether or not tasks like the pen-and-cups task do demonstrate goal-directed imitation, and therefore, whether they can be used to support the claims of GOADI and specialist theories. This issue is investigated in Chapter 2 of this thesis.

1.3.3 Atypical development

The relationship between atypical development and imitative abilities is highly relevant to the topics discussed in this thesis. This section addresses imitative abilities in autism spectrum disorder (ASD) and whether evidence of impairments in this population can inform theories of imitation.

Autism spectrum disorders are developmental disorders which are characterized by abnormalities of social interaction, impairments in verbal and non-verbal communication, and a restricted repertoire of interests and activities (American Psychiatric Association (APA), 1994). Three main cognitive theories have been suggested to explain the core deficits associated with ASD. These are the theory of mind hypothesis (e.g. Baron-Cohen, Leslie & Frith. 1985; Frith, 2003; Frith & Frith, 2003; Gallagher & Frith, 2003; Happé, Ehlers, Fletcher, Frith, Johansson, Gillberg, Dolan, Frackowiak & Frith, 1996), the weak central coherence account (e.g. Happé, 1999; for alternative views see: Mottron, Peretz & Menard, 2000; Plaisted, 2001) and the theory of executive dysfunction (e.g. Pennington, & Ozonoff, 1996; Russell, 1997; Ozonoff, Pennington & Rogers, 1991). More recently, it has been suggested that impairments in imitative abilities underlie ASD (e.g. Rogers & Pennington, 1991; Rogers, 1999; Williams, Whiten & Singh, 2004). This theory and its implications for our understanding of imitation will be discussed in this section.

As highlighted in Section 1.3, special-purpose mechanisms should be susceptible to selective impairment (e.g. Fodor, 1983; Leslie, 1992). That is, an impairment in one domain that is not associated with more generalised deficits. Therefore, the presence of a selective imitation impairment in ASD may provide support for a special-purpose mechanism in imitation. Findings from atypically developing populations have been used to address the issue of modularity in the past. Previous theorists have used evidence of a selective impairment in a specific competency to argue in favour of innately specified, specialised brain circuits for that competency (e.g. Bellugi, Wang & Jernigan, 1994; Gopnik, 1990; Leslie, 1992; 1998; Pinker, 1994). For example, evidence of 'theory of mind' impairments in ASD in the absence of general intellectual impairments has been cited as evidence for a theory of mind module (Leslie, 1992; 1998). The same logic, if applied to imitation, would suggest that imitation impairments in ASD support specialist claims.

Findings from a number of studies have suggested that imitation impairments are both universal and specific in ASD (Charman, Swettenham, Baron-Cohen, Cox, Baird & Drew, 1997; Dawson & Adams, 1984; DeMyer, Alpern, Barton, Deyer, Churchill, Hingtgen, Bryson, Pontius & Kimberlin, 1972; Hammes & Langdell, 1981; Jones & Prior, 1985; Ohta, 1987; Rogers, Bennetto, McEvoy, & Pennington, 1996; Sigman & Ungerer, 1984; Stone, Ousley, & Littleford, 1997; Whiten & Brown, 1998). In the most recent review of the literature, Williams et al. (2004) reviewed 17 experimental studies on imitation in ASD. They calculated the combined p-value of group differences with respect to imitation to an appropriate control group: $p < 0.00005$ (n = 248 subjects). The authors reinforced Rogers et al's previous (1999) message that "every methodologically rigorous study so far published has found an autism-specific deficit in imitation" (p. 294, Williams et al., 2004).

Imitation impairments have been demonstrated in object-directed actions (Hammes & Langdell, 1981; Roeyers, Van Oost, & Bothuyne 1998; Stone et al., 1997; Whiten & Brown, 1999), pantomime actions (Hammes & Langdell, 1981; Whiten & Brown, 1999), body movements (Stone, Lemanek, Fishel, Fernandez, & Altemeier, 1990), gestures (Aldridge, Stone, Sweeney, & Bower, 2000; Whiten & Brown, 1999), sequential imitation (Rogers et al., 1996), novel actions (Roeyers et al., 1998), and meaningful and meaningless actions (Stone et al., 1997). These impairments have been found in children (e.g. Rogers et al., 1996) and in adults (Avikainen et al., 2003).

The reported impairments have led some researchers to suggest that imitation is the core impairment in ASD (Williams et al., 2004). This claim has been extended in the mirror neuron hypothesis of ASD, which supposes that the mirror neuron system, thought to mediate imitation, is disturbed in individuals with ASD (Williams, Whiten, Suddendorf & Perrett, 2001). Mirror neurons and imitation have been suggested to underpin the development of language and social cognitive functions, such as theory of mind and empathy (Gallese & Goldman, 1998; Rizzolatti & Arbib, 1998; Rogers & Pennington, 1991). Impairments in these abilities characterise ASD which has led theorists to suggest that an imitation impairment, caused by a dysfunctional mirror system, leads to a developmental cascade of impairments in these other abilities. Under this view, mirror neuron system and imitation impairments are at the root of ASD.

Some evidence of mirror system abnormalities has been demonstrated using neuroimaging techniques, although many of the results from these studies are inconsistent. For example, structural abnormalities in mirror areas have been demonstrated in the brains of individuals with ASD although these abnormalities were not specific to mirror areas (Hadjikhani, Joseph, Snyder, & Tager-Flusberg, 2006).

Furthermore, differential neural activation in mirror areas has been demonstrated in ASD. Nishitani, Avikainen, & Hari (2004) studied motor cortex excitability using MEG and found differential activation patterns in individuals with ASD compared to typically developing controls when imitating orofacial movements, which implies mirror system abnormalities. However, Avikainen, Kulomaeki, and Hari (1999) found no difference in activity between ASD and control participants when observing simple hand movements suggesting typical mirror system activity in the ASD group.

Contrary to this finding, Obermann, Hubbard, McCleery, Ramachandran & Pineda (2005) reported an absence of mu-wave suppression, which is thought to be modulated by the mirror system, when participants with ASD observed simple hand actions. While this finding may suggest reduced mirror system activity it could result from poor connectivity between the mirror system and primary motor cortex. The latter explanation is consistent with results of a number of studies reporting weaker connectivity in ASD (Bird, Catmur, Silani, Frith, & Frith, 2006).

Theoret, Halligan, Kobayashi, Fregni, Tager-Flusberg & Pascual-Leone (2005) found reduced motor-evoked potentials (MEPs) in response to action observation in individuals with ASD. However, the reduction in MEPs only occurred when actions were observed from the 'self' perspective (fingers pointing away from the participant). When actions were observed from the 'other' perspective (fingers pointing towards the participants) MEPs were not different between the ASD and control groups, making this finding difficult to interpret.

Further inconsistent findings have been demonstrated using fMRI. Williams, Waiter, Gilchrist, Perrett, Murray & Whiten (2006) compared neural responses during

imitation tasks between individuals with ASD and control participants. They found greater activity in parietal, but not inferior frontal, cortex in the control group. However, Dapretto et al. (2006) reported the opposite pattern of results demonstrating that individuals with ASD show normal activity in the parietal mirror area but reduced activity in the inferior frontal gyrus. Dapretto et al. (2006) also provided further evidence of a mirror system impairment in ASD by showing a correlation between mirror system activity and autistic symptom severity.

Reported imitation impairments combined with evidence of mirror neuron dysfunction implies impairment of imitation and the brain structures dedicated to imitation in ASD. In ASD, other aspects of the cognitive system are often relatively preserved. For example, there are many cases of autistic symptoms in the presence of IQ within and even above the normal range. Consequently, this may imply that imitation is susceptible to selective impairment which may provide support for the idea that a special-purpose mechanism mediates imitation. However, in order to use such evidence to support specialist theories, it is necessary to demonstrate that there is selective impairment in that domain, that is, it is not a product of other more generalised deficits. In order to do this, it is necessary to address some inconsistencies in the literature.

As highlighted above, findings from the neurological literature are somewhat inconsistent. Until studies investigating mirror system activity show a more consistent pattern, it is unlikely to be possible to relate them coherently to behavioural investigations of imitation in ASD. In addition to the confusion in the neurological literature, there is further confusion in the behavioural literature. Despite the large body of research on the topic, it is not yet clear whether there is a real imitation

impairment in ASD. First, there are some inconsistencies in the literature with some authors failing to find a deficit (e.g. Beadle-Brown & Whiten, 2004; Charman & Baron-Cohen, 1994; Hamilton, Brindley & Frith, 2007; Morgan, Cutrer, Coplin & Rodrigue, 1989). Second, many of the early studies contained methodological flaws such as inadequate control group matching (e.g. Sigman & Ungerer, 1984) or insufficient diagnostic information (e.g. DeMeyer et al., 1972).

Third, the finding of an imitative impairment in imitation is puzzling in light of anecdotal evidence reporting echolalia and echopraxia in ASD. The observation of echolalic (the tendency to automatically imitate the speech patterns of others with no discernable goal), and echopraxic (the tendency to automatically imitate the actions of others) phenomena (Russell, 1997) imply that individuals with ASD have an increased tendency to imitate rather than a deficit.

A possible explanation for these inconsistencies in the literature could be the type of tasks used to measure imitative ability. The majority of tasks used to date are complex intentional or voluntary imitation tasks, presented in a rich social context. Successful performance on these tasks relies on a number of other processes such as understanding of social cues, language ability, theory of mind, perceptual processing of complex stimuli, attentional control, motor control and executive function. These processes are not imitation-specific abilities; they are necessary for a range of imitative and non-imitative tasks. Therefore, poor performance on tests of imitation may be due to impairments on these non-specific abilities. Consequently, there may not be an imitation-specific impairment in ASD, but rather any apparent imitation impairment may be a symptom of other more generalised impairments.

There are a number of candidate non-specific abilities that may contribute to poor performance on imitative tasks. First, the impairments could simply reflect a lack of motivation to engage in imitative exchanges. This idea is consistent with evidence highlighting the reluctance to participate in social activities in ASD (e.g. Kanner, 1943; Kanner & Eisenberg, 1956). Some evidence in favour of this idea is provided by Ingersoll, Schreibman & Tran (2003) who examined the effect of sensory feedback (e.g., flashing lights and sound) on the imitation performance of children with ASD and age matched controls. They found that sensory feedback improved imitative performance of the children with ASD but not controls and argued that children with ASD are less motivated by social interaction to imitate, but may be motivated to imitate if they receive a non-social reward.

Second, task demands such as executive function, working memory, attentional control, perceptual and motor abilities that are necessary for complex imitation tasks may explain poor performance. Deficits in all of these abilities have been reported in individuals with ASD (e.g. Bertone, Mottron, Jelenic & Faubert, 2003; Greenaway & Plaisted, 2005; Ghazuiddin & Butler, 1998; Ghazuiddin, Butler, Tsai & Ghaziuddin, 1994; Gillberg, 1989; Hill, 2004; Leary & Hill, 1996; Manjiviona & Prior, 1995; Rinehart Bradshaw, Brereton & Tonge, 2001; Russel, Jarrold & Henry, 1996).

Some evidence in favour of this view has been provided by Vanvuchelen, Roeyers & De Weerdt (2007) who found that children with ASD performed poorly compared to matched controls on a number of imitation measures. However, imitation performance was strongly correlated with general motor ability. Similarly, Motofsky, Dubey, Jerath, Jansiewicz, Goldberg & Denckla (2006) found that children with ASD were impaired on gestural imitation compared to age and IQ matched controls. However, they were

similarly impaired when required to make a gesture in response to a command and in a tool use task. The authors suggested that ASD is associated with a generalized praxis deficit rather than a deficit specific to imitation. Other authors have provided similar findings suggesting that imitative performance is strongly related to other non-specific abilities such as social reciprocity and attention following (Green, Baird, Barnett, Henderson, Huber & Henderson, 2002; McDuffie, Turner, Stone, Yoder, Wolery, & Ulman, 2007; Smith & Bryson, 1998).

However, while the foregoing studies demonstrate positive correlations between imitation performance and other more general abilities, not all of the reported deficit in imitation can be explained by these other abilities. While in one study 80 percent of variance in imitation scores could be accounted for by motor abilities (Vanvuchelen et al., 2007), Smith & Bryson (1998) found that motor impairment accounted for only 37 percent of the variance in imitation performance. Therefore, it is not clear from these studies whether the non-specific impairments are able to fully account for the observed imitation impairment. Consequently, it is not clear whether there is an imitation impairment over and above impairments in other more general processes.

The inconsistencies highlighted above suggest that the present literature is not yet able to reliably demonstrate the existence of an imitation-specific impairment in ASD. It is important to try to resolve this confusion in the literature, both in order to better understand the core impairments in ASD and also to understand how this issue relates to imitation theories.

In order to clarify these issues Chapters 3 and 4 investigated imitative abilities in adults with ASD. Chapter 3 investigated whether observed impairments in imitation

can be accounted for in full by deficits in processes not specific to imitation using an intentional imitation task. Given that complex imitation tasks require a number of abilities in addition to imitation, Chapter 4 investigated imitative abilities in ASD using a 'purer' test of imitation. In this test, task requirements were reduced, such that demands placed on other processes that contribute to performance were minimised. In order to reduce task requirements, an automatic imitation task was used in Chapter 4.

In tests of intentional imitation, the experimenter asks the participants to copy an action that has many spatial and temporal features and does not specify the exact features to be reproduced. Therefore, successful performance depends, not only on a willingness to co-operate with the experimenter, but also on appropriate selection of action dimensions for imitation using contextual, including social, cues for which dimensions are relevant in any particular task. A more appropriate way to investigate imitation abilities in ASD, therefore, is to use a simple task where imitation is not instructed, that is an automatic imitation task. In tests of automatic imitation, participants are not asked, and do not intend, to imitate modelled movements. Instead, they are required to merely observe actions, either passively or with a simple movement task, while the experimenter measures muscle responses (Heyes, Bird, Johnson & Haggard, 2005). Automatic imitation tasks place fewer demands on task-general abilities and would constitute a purer test of imitative ability. Therefore, these tasks may be particularly appropriate for assessing imitative ability in ASD. Automatic imitation tasks of this type have been used to investigate imitation in typically developing adults and the findings from these studies are highlighted below.

1.3.4 Imitation in adults

1.3.4.1 Automatic imitation

A tendency to imitate the actions of others involuntarily or 'automatically' is of relevance to imitation theories. Both generalist theories addressed in this thesis suggest that observation of an action performed by someone else automatically leads to an activation of an internal motor representation. Therefore, ASL and IM predict that under some circumstances imitation may occur automatically, that is without intention (Heyes, 2005; Prinz, 2005). The following studies demonstrate the occurrence of automatic imitation and therefore provide support for both of the generalist theories addressed in this thesis.

Recent electrophysiological studies have demonstrated motor facilitation by action observation (e.g. Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Catmur, Walsh & Heyes, 2007; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Strafella & Paus, 2000). In these studies, passive participants observed body movements while transcranial magnetic stimulation (TMS) induced MEPs were recorded from a range of muscles. It was found that MEPs recorded from the muscles involved in execution of the observed movement were greater than those recorded at other muscle sites.

The foregoing examples provide some evidence of a tendency to imitate automatically, but this was only detected in cortical and muscular activation. Evidence of overt unintentional imitation comes from research examining the 'Chameleon effect' in relatively unconstrained social interactions (e.g. Chartrand & Bargh, 1999; Lakin & Chartrand, 2003). Participants in these studies are asked to interact freely with another individual whom they believe is a participant, but who is actually a confederate. The

confederate exhibits a target behaviour during the interaction, such as tapping their foot or rubbing their face. The results consistently showed that participants were more likely to rub their face in the presence of a face-rubbing confederate than a foot-shaking confederate and to shake their foot in the presence of a foot-shaking confederate than a face-rubbing confederate. During post-test debriefing, participants reported that they did not notice the target behaviour being demonstrated, that they had no intention to imitate the behaviour, and that they were unaware of doing so.

Research using stimulus-response compatibility (SRC) paradigms also implies that movement observation can induce the observer to prepare to perform a matching movement even when performance of such a movement would be detrimental to task performance (Brass et al., 2000; Craighero, Fadiga, Rizzolatti, & Umilta, 1998; Heyes et al., 2005; Stürmer, Aschersleben, & Prinz, 2000). For example, Brass et al. (2000) asked participants to lift (in one test block), or lower (in another test block) their index finger as soon as they saw a movement of a stimulus hand (the imperative stimulus). In this simple RT procedure, participants were always required to perform the same movement throughout a block, irrespective of the stimulus movement. Stimulus movements were either compatible (e.g. finger lift response and finger lift stimulus), or incompatible (e.g. finger lift response and finger tap stimulus) with respect to the response movement. Participants were faster to respond on compatible than incompatible trials, suggesting that perception of an action primes production of that action even when the identity of observed movements is technically task-irrelevant. More recent investigations have demonstrated that effects of this kind are not solely due to spatial compatibility (e.g. Bertenthal, Longo & Kosobud, 2006; Brass et al., 2001; Heyes et al., 2005; Press, Gillmeister & Heyes 2006; Press, Bird, Flach & Heyes, 2005; Press, Bird, Walsh & Heyes, under review).

The preceding studies demonstrate 'movement compatibility' effects, such that, execution of a particular movement is faster when accompanied by observation of a compatible movement than when it is accompanied by observation of an incompatible movement. In real life instances of imitation we tend to match both the movement made as well as the effector used to make that movement. Therefore, it should be possible to demonstrate automatic imitation of both movement and effector. 'Effector compatibility', where observation of a particular effector in motion facilitates a motor response with the matching effector, has not been directly investigated. However, studies investigating 'effector priming' effects suggest that we do automatically match the effector used (Berger & Hadley, 1975; Bertenthal et al., 2006; Brass et al., 2000; Gillmeister, Catmur, Brass & Heyes, under review). This issue will be explored further in Chapter 5.

The studies carried out to date demonstrate unintentional activation and/or production of observed body movements. These data are consistent with generalist theories which claim that action observation automatically leads to motor activation. Furthermore, automatic imitation may be inconsistent with some specific claims made by AIM and GOADI. Both theories suggest that imitation occurs via intentional, rather than automatic, processes (Neumann, 1984). AIM makes this explicit stating that imitation is an 'active' process (Meltzoff & Moore, 1994). That is, when a body movement is observed *with the intention to imitate*, the visual representation is converted into a supramodal code allowing a matching motor output to be generated (Meltzoff & Moore, 1997). If as AIM suggests, the intention to imitate is a necessary component of imitation, we should not observe instances of automatic imitation. It should be noted, however, that Meltzoff has recently contradicted this earlier statement by asserting that the same mechanisms that mediate imitation in newborn infants, mediate automatic

motor facilitation following action observation (Meltzoff & Decety, 2003). This clearly implies that the occurrence of automatic imitation is not inconsistent with AIM, however, Meltzoff & Decety did not explain how AIM is able to accommodate its occurrence.

A goal-directed view of imitation would also seem to be at odds with evidence of automatic imitation since this view implies conscious and effortful processing. However, it is not clear in GOADI or AIM whether the goal selection processes thought to mediate imitation operate at a conscious level or automatically. It may be that we automatically represent actions in terms of goals. Therefore, it is not apparent whether or not GOADI and AIM can account for automatic imitation.

Nevertheless, Brass & Heyes (2005) suggested that evidence of automatic imitation is inconsistent with the idea that a special-purpose mechanism mediates imitation stating that "one would expect an efficient specialist imitation mechanism to be 'switched on' only when needed", that is, only when one intends to imitate. However, it has been argued that special-purpose mechanisms are automatically activated (Fodor, 1983). Therefore, in the case of imitation, the intention to imitate may not be critical in eliciting this activation. It is more likely that special-purpose mechanism would be 'switched on' by a specific class of stimuli. This is in line with domain specificity - the requirement that special-purpose mechanisms deal exclusively with a single type of information (Fodor, 1983). The following section addresses this issue.

1.3.4.2 Animacy

Special-purpose mechanisms are commonly assumed to be domain specific (Fodor, 1983), that is, they deal with a specific type of information. In the case of imitation it is likely that observed human action constitutes the relevant domain of information. Therefore, if imitation is mediated by such a special-purpose mechanism then we should expect it to be especially efficient in processing human action stimuli.

There is some evidence that human action stimuli are more effective at eliciting imitative responses than robotic stimuli. In an interference paradigm, Castiello, Lusher, Mari, Edwards & Humphreys (2002) found that observing human, but not robotic, movements influenced subsequent performance of similar reaching and grasping movements. Similarly, Castiello (2003) found that the movement dynamics of an observing participant were influenced by a distracter object when the action was carried out by a human model but not when it was carried out by a robotic model.

Using an automatic imitation paradigm of a different kind, Kilner, Paulingnan & Blakemore (2003) and Oztop, Franklin, Chaminade & Gordon (2005) found a stronger tendency to imitate human than robotic movements. Participants were required to perform sinusoidal arm movements in one direction (e.g. vertical) while simultaneously observing human or robotic movements in a compatible (vertical) or incompatible (horizontal) direction. Participants displayed more variance in the pathway of movements when concurrently observing human movements in an incongruent direction, compared with a congruent direction. However, this automatic imitation effect was found to be smaller (Ozrop et al., 2004), or not present (Kilner et al., 2003), when concurrently observing robotic movements.

An fMRI study has supported the idea that human movement stimuli are more readily imitated than robotic movement stimuli by showing more activation of cortical areas thought to mediate imitation when observing human movements than when observing robotic movements (Tai, Scherfler, Brooks, Sawamoto & Castiello, 2004). This finding is compatible with other imaging studies which have shown increased activation of cortical areas associated with imitation in response to observing human stimuli compared to unnatural stimuli (e.g. Stevens, Fonlupt, Shiffrar & Decety, 2000) and animal action stimuli (Buccino et al., 2004).

Some of the foregoing studies, therefore, appear to provide support for specialist theories. However, generalist theories can also explain an effect of animacy on imitation. Under ASL, sensorimotor links are formed through concurrent experience of seeing and doing. Since we are unlikely to have gained a great deal of experience of seeing a robot performing an action while performing an action ourselves, these links would not have had a chance to form, and therefore, we would not expect imitation of robots. However, an important feature of associative learning is stimulus generalisation: the effects of learning with a particular stimulus are not only present in behaviour toward that stimulus, but also in behaviour elicited by other stimuli to the extent that those stimuli have physical characteristics in common with the learned stimulus (Pearce, 1994; 1987). Similar predictions would be made by IM which states that action observation primes performance of an action to the extent that the observed and executed actions have similar sensory consequences.

Therefore, a generalist account would expect some imitation of non-human stimuli to the extent that they share features with human stimuli. Some evidence in support of this idea has recently been presented by Press et al. (2005; 2006). Using a SRC

paradigm to investigate automatic imitation, the authors found some evidence of automatic imitation of robotic stimuli. In a simple RT task participants were required to carry out an open or closed movement in response to human or robotic movements. A compatibility effect was observed such that open responses were made faster in response to open stimuli than closed stimuli and vice versa. This automatic imitation effect was present both for human and robotic stimuli, although the effect was greater for human stimuli.

Although there are some mixed findings in this area of the literature, many of the studies reported show at least some imitation of non-human stimuli (e.g. Oztop et al, 2004; Press et al., 2005; 2006). Therefore, the foregoing studies may be more consistent with generalist theories than specialist theories. The following section provides additional support for generalist theories by examining the role of experience on imitation.

1.3.4.3 Training and expertise

Generalist theories, particularly the ASL model, predict that whether and how well a person imitates will depend on their past experience. Imitation of an observed action is only possible if the opportunity to form a link between visual and motor representations of action components arises. Specialist theories do not explicitly deny the importance of learning, but the AIM model suggests that the capacity to imitate is innate. Since in this model, the links between sensory and motor representations did not arise through learning, but rather are hard-wired, it seems unlikely that they should be modifiable by experience. Furthermore, at least one prominent author has explicitly stated that learning would not be expected to have a significant impact on innate special-purpose mechanisms: Pinker (1997) argued that experience-based alteration of

special-purpose mechanisms would usually be maladaptive, and therefore natural selection is likely to have acted to prevent such modification. Therefore, studies demonstrating the effects of learning and experience on imitation are more consistent with generalist than with specialist theories.

Evidence from several behavioural studies shows that, as generalist models predict, familiar actions are imitated more successfully than novel actions (Tessari & Rumiati, 2002; 2004). Participants make fewer errors while carrying out actions such as combing their hair, than they do while carrying out unfamiliar actions where similar movement components were executed near a different part of the body (e.g. on the torso). In a follow up investigation, the authors found that, when participants practised imitating the unfamiliar actions, their performance improved such that they were as accurate on these actions as the previously familiar actions.

The ASL model proposes that correlated sensorimotor experience is necessary for sensorimotor links to be formed. A number of studies demonstrate modification of imitation following sensorimotor training which provides additional support for generalist theories (Gillmeister et al., under review; Press et al., 2006; Heyes et al., 2005). For example, a training study conducted by Heyes et al. (2005) controlled for levels of perceptual and motor experience and observed effects of correlated visual and motor experience. During a training phase, Heyes et al. (2005) required half of the participants to open their hand as soon as they saw a stimulus hand begin to open, and to close their hand as soon as they saw a stimulus hand close (compatible training group). The other half were required to open their hand as soon as they saw a stimulus hand begin to close and to close their hand as soon as they saw a stimulus hand open (incompatible training group) and vice versa in each case. In the subsequent test

session participants in the compatible group showed an automatic imitation effect. That is, in a simple RT task, the participants were faster to execute a pre-specified action (e.g. opening the hand) when it was compatible with the observed action (opening) than when it was incompatible (closing). In contrast, the incompatible group did not show an automatic imitation effect. Thus, training resulted in a modification of the connections between perceptual and motor representations. This study demonstrates that experience can influence imitation of a stimulus suggesting that links between sensory and motor representations arise through experience, thus supporting generalist claims.

In addition to these studies highlighting the effects of training on overt imitative behaviour, some recent studies have demonstrated the effects of training or experience on the mirror neuron system, thought to subserve imitation. While mirror neurons may represent the link between sensory and motor representation, it is not yet clear how these neural areas acquired their mirror properties. It is assumed by specialist theories that mirror neurons are 'for' imitation i.e. that natural selection has endowed these mirror areas with their imitative properties. Under this view, mirror neurons themselves are the special mechanism which performs the match or translation of sensory information into motor output. An alternative view is presented by generalists who claim that mirror neurons can 'do' imitation but are not necessarily 'for' imitation. Generalists suggest that mirror neurons acquire their mirror properties during development as a side-effect of general associative learning processes (see Keysers, & Perrett, 2004 for a similar view). Under this view, the only reason mirror neurons become 'mirror' neurons is because the environment provides opportunities to associate visual and motor representations of the same action. Mirror neurons could

theoretically link completely arbitrary (non-matching) sensory and motor representations given the appropriate experience.

Some evidence in support of this generalist view has been provided in a recent TMS study by Catmur et al., (2007), where participants were required to passively observe little and index finger movements while TMS was applied to their motor cortex. During an initial test phase, increased MEPs were recorded in the little finger following observation of little finger movements and in the index finger following index finger movements. Participants were then given either compatible sensorimotor training or incompatible sensorimotor training. The compatible training group repeatedly performed little finger movements while observing little finger movements and index finger movements while observing index finger movements. The incompatible training group repeatedly performed little finger movements while observing index finger movements and index finger movements while observing little finger movements. In the post-training phase the original effect in the incompatible group was reversed such that increased MEPs were recorded in the little finger following observation of index finger movements and in the index finger following little finger movements.

Other functional imaging studies support the hypothesis that training and expertise can influence activation in mirror areas. Calvo-Merino, Glaser, Grezes, Passingham & Haggard (2005) conducted an fMRI study with expert ballet and capoeira dancers to investigate influences of expertise on activation of motor cortices when observing action. The authors found that when participants (e.g. ballet dancers) were observing dance actions which they had been trained to perform (ballet movements), there was greater activation in premotor and parietal cortices than when they were observing

actions which they had not been trained to perform (capoeira movements). Cross, Hamilton & Grafton (2006) observed similar effects of expertise in dancers.

Therefore, the foregoing studies provide some support for generalist theories of imitation, in particular the ASL model. These findings suggest that general learning mechanisms and environmental input are sufficient to account for imitative abilities.

1.4 Summary

The main purpose of this thesis is to investigate how observation of action facilitates production of matching movements. Therefore, this thesis addresses *how* we are able to imitate and whether this question may be better answered by specialist or generalist theories of imitation. In order to do this, Chapters 2, 3 and 4 challenge some evidence that has been put forward to support specialist claims. The final experimental chapter provides some specific support for generalist theories.

Chapter 2 examines the role of mentalistic goals in imitation using the pen-and-cups task. This chapter aims to distinguish between a goal-directed account of imitation and a generalist account of imitation and therefore challenges some evidence in favour of GOADI. Chapters 3 and 4 examine another line of evidence that may be consistent with a specialist view of imitation, that is, the reported imitation impairment in ASD. Chapter 3 employs the pen-and-cups task to examine intentional imitation abilities in adults with ASD. In Chapter 4, imitative ability of individuals with ASD is examined using an automatic imitation paradigm.

Finally, Chapter 5 provides specific evidence in support of generalist theories by investigating effector-specificity in imitation. In everyday life and in experimental

examples, imitation is effector-specific; that is we imitate hand movements with our hands and foot movements with our feet. This effector-specificity may be able to inform us about the structure of the core mechanisms of imitation. This chapter distinguishes specialist from generalist theories by investigating claims made by ASL, IM and AIM concerning the degree of effector-specificity that should be present in imitation.

In summary: this thesis examines the question of whether imitation is mediated by special-purpose or task-general psychological processes. To this end, the experiments reported in Chapters 2-5 used both intentional and automatic imitation tasks and these tasks have been used to test typically developing individuals and individuals with ASD.

Chapter 2: Intentional imitation in typically developing individuals: Are 'mentalistic goals' necessary to explain how we imitate?

The aim of this thesis is to address the question of *how* we are able to imitate. This question raises a fundamental problem since successful imitation requires a translation of sensory information received from observing an action into the motor commands necessary to carry out a matching action (the correspondence problem, Brass & Heyes, 2005).

Many researchers have suggested that 'goals' guide imitative behaviour (e.g. Byrne, 1993; 2003; Meltzoff, 1995; Meltzoff & Moore, 1997; Wohlschläger et al., 2003). Goals and their relationship to imitation may be relevant when trying to explain how the correspondence problem is solved. Goal-directed theories of imitation suggest that intermediate recoding occurs between observation and execution of a body movement. These theories imply that, in addition to the visual representation of the observed movement and the motor representation that drives muscle movement, imitation involves a third kind of representation. This third type of representation is neither sensory nor motor, but is rather at the level of the goal of the act. When we observe an action, we do not try to sequence the action elements observed into specific movements made; rather we extract the goal of the action. Consequently, such action goals make it possible for a relevant motor programme to be activated. Goals, potentially, represent the link between the seen but unfelt and the felt but unseen, and therefore they may be the solution to the correspondence problem (e.g. Bekkering & Wohlschläger, 2002; Byrne, 1993; Byrne & Russon, 1998; Meltzoff & Moore, 1997). The aim of this chapter is to investigate the role of goals in imitation and to discover whether goals can provide an explanation for how we imitate.

Both of the specialist theories addressed in this thesis highlight the role of goals in imitation, and GOADI provides an explicit statement of this view. According to GOADI (e.g. Bekkering et al., 2000; Gleissner et al., 2000; Wohlschläger & Bekkering, 2002; Bekkering & Wohlschläger, 2002), goals are extracted from perceived movements. The goal representation then activates its most commonly associated motor program, irrespective of whether this matches the movement performed by the model. Similarly, under the AIM model (e.g. Meltzoff & Moore, 1997), perceived actions are actively processed in order to infer the model's goals. These goals are then translated into supramodal representations which are used to produce motor commands.

As discussed in Chapter 1, a number of findings have been argued to demonstrate the role of goals in imitation and thus provide specific support for GOADI. These findings demonstrate that, when required to imitate, children and adults frequently perform movements that systematically differ from the model's movements. It appears that, instead of faithfully reproducing all aspects of a movement, individuals reproduce the goal of that movement. Bekkering and colleagues have investigated how the goal of an action (such as touching a dot on a table, or placing a pen in a cup) affects the translation from perception to action and have shown that children and adults primarily focus on reproducing the goal of the action and not on reproducing the means used (Bekkering et al., 2000; Wohlschläger et al., 2003). For example, the pen-and-cups task allows three components of action to be manipulated independently: object selection, effector selection and grip selection. On each trial in this speeded response procedure the participant sees a model move a centrally located pen into one of two coloured cups (object), using his right or his left hand (effector), while grasping the pen with his thumb pointing up or down (grip). Adults typically make fewer cup errors

than hand errors and fewer hand errors than grip errors (Avikainen et al., 2003; Wohlschläger & Bekkering 2002). If one supposes that the primary goal of each action is to place the pen into a cup, then this cup<hand<grip error pattern supports the view that participants code an action in terms of its goal, and when processing resources are limited, this goal is more accurately reproduced than the means by which the goal is achieved. This view has been supported by a number of other similar findings (Gleissner et al., 1999; Gattis et al., 2002; Head, 1963; Want & Gattis, 2005).

However, one critical issue is the exact meaning of the term 'goal', since the term has been used in a variety of contexts across the literature. While some authors assume that it refers to an observable, physical, end-state or outcome, others imply that it is a more mentalistic concept relying on intention understanding. Under the latter view, theory of mind abilities are needed to infer a model's goals. For example, Wohlschläger and colleagues (2003) suggest that goals are action outcomes or end-states, stating that "although using action goals as the core concept, GOADI does not say anything about the representation of the intentions of the model in the imitator. In our view the representation of intentionality or any theory of mind is not necessary to explain imitation". However, a contrasting claim was made by Gattis et al. (p202, 2002) who explicitly stated that "goals are mental states". Under this view, a goal is understood to be the inferred intention of the model and this view represents a mentalistic interpretation of the GOADI model (henceforth mGOADI).

Thus, according to goal-directed theories, any recoding between perception and action may represent either physical, end-state goals or mentalistic goals. Some recent evidence, however, suggests that actions are not always coded in terms of physical, end-state goals. Bird et al. (2007) carried out a series of experiments using the pen-

and-cups task and demonstrated that the cup<hand<grip error pattern could be altered such that the outcome of an action was not always the most accurately imitated component. Whereas in the original version of the pen-and-cups task, the cup component is the only component that is differentially coloured (i.e. one cup was coloured blue and the other red), Bird and colleagues manipulated the colour coding such that either the cup, hand or grip component was differentially coloured. For example, in one condition, the cups were both a neutral colour but the model and participant wore coloured gloves, such that one hand was blue and one was red. Altering which component was coloured resulted in a modification of the error pattern such that the coloured component was always the most accurately reproduced component ('colour minimum error pattern'). Thus, the means (hand or grip selection) of carrying out an action were more accurately imitated than the end-state or *goal* (cup selection) of that action.

The authors suggested that it is not necessary to represent physical end-state goals in order to translate observed actions into executed actions. Rather, imitation performance on this task can be explained by more general, perceptual and attentional processes. The authors suggested that differentially colouring a particular component enhances the discriminability of that component and this perceptual enhancement, rather than goal attribution, explains error patterns in this task.

Thus, if goals are understood to be physical end-states, then Bird et al's results undermine the hypothesis that observed actions are always coded as goals for imitation. However, if goals are understood to be intentions, the results of Bird et al. do not bear directly on the goal-directed hypothesis. It is possible that shifting the colour cue in the pen and cups task induces a revision of the imitator's inferences about the

model's intentions. For example, adding colour to the hand may have resulted in the observed action being coded as, "The model intends to grasp the pen with his *red hand* and put it in a cup", rather than, "The model intends to place the pen in the *red cup*" when the cups are coloured. Therefore, the colour minimum error pattern reported by Bird et al. may have been due to inferences about the model's intentions. Under this interpretation of GOADI, actions are represented in terms of mentalistic goals, which is in line with the mGOADI variant of the model forwarded by Gattis et al. (2002).

Support for the idea that mentalistic goals are intrinsic to imitation has been provided by a number of authors. In a study by Meltzoff (1995), infants either observed a demonstrator successfully carrying out a target action on an object or attempting to carry out the action but failing to do so. For example, the demonstrator attempted to pull apart a dumbbell-shaped toy but their hand 'accidentally' slipped off one end of the dumbbell, such that they did not successfully pull it apart. Meltzoff found that 18-month-old infants produced target acts as frequently following observation of these "failed attempts" as they did following observation of the demonstrator successfully completing the target actions. Meltzoff concluded that 18-month-old infants represent an action in terms of the intended goal and it is this goal that is imitated rather than specific movements.

In a second experiment, infants were shown a mechanical device with two pincers that mimicked the way the demonstrator had acted on a dumbbell-shaped toy in the failed-attempt display (Meltzoff, 1995). Pincers grasped the dumbbell on the two ends and pulled them outward, but one pincer slipped off one of the two ends. After watching the unsuccessful acts demonstrated by the mechanical device, infants pulled the dumbbell apart less frequently than when the same action was demonstrated by a

human actor. Given that attribution of intentions is unlikely when observing a mechanical device, this finding represents further evidence that infants' imitation of target acts in failed attempt conditions is due to the tendency to code actions in terms of the underlying intention of the model and to imitate that intention, rather than faithfully to copy the action demonstrated.

However, it could be argued that intention reading is not necessary to explain the results from the foregoing studies; general-purpose mechanisms rather than mental-state goal inferences could explain imitation in these instances. For example, rather than demonstrating that infants were reading and copying the intentions of the actor, behavioural reproduction of a modelled action may occur when observation of the manipulations of the demonstrator draws an individual's attention to relevant parts of objects. Thus, the individual learns to adjust to specific environmental features without learning about the observed actions (Tomasello, 1996; Whiten & Ham, 1992).

Some evidence in support of this hypothesis has been provided by Huang, Heyes & Charman (2002), who examined the role of general processes in a failed attempts paradigm. To do this, they replicated Meltzoff's (1995) study and included two additional conditions. First, in a novel emulation learning condition, infants were exposed to the initial and end states of the target display but not to the experimenter's manipulations of the test objects (which were occluded by a screen). Second, in the spatial contiguity condition, the experimenter moved the two individual parts of the object set to bring them in close proximity so that the target-relevant parts were spatially contiguous with each other. It was demonstrated that infants in the emulation-learning and spatial contiguity conditions produced as many target acts as infants in the

full-demonstration and failed-attempt conditions. This suggested that intention reading was not necessary to explain the results from failed attempt studies.

Therefore, findings which purport to show that mentalistic goals are intrinsic to imitation can also be explained with reference to general processes. This 'general process account', claims that the mechanisms that mediate perception and attention to visual stimuli in a range of tasks, both imitative and non-imitative, are sufficient to explain the findings that are commonly understood to support a goal-directed view. Therefore, representing the intentions of the model is not necessary to explain certain imitative behaviour. For example, when one's attention is drawn to a particular aspect of a movement, one may be more likely to reproduce this aspect, without representing the intentions of the model. Alternatively, if a particular component of a movement is differentially coloured, such as the two cups in the pen-and-cups experiments, one may be more accurate in reproducing this component because it is easier to discriminate one cup from the other.

This general process account is consistent with a generalist view of imitation which supposes that there are no imitation-specific processes. A generalist account of imitation would therefore deny the involvement of imitation-specific goal attribution processes. Consequently, the general process account both challenges claims made by specialist theories about the intrinsic role of goals in imitation and is also consistent with generalist theories of imitation. Thus, investigating whether goals or general processes better account for imitation behaviour is highly relevant to the topics discussed in this thesis.

The aim of this chapter is to distinguish between goal-directed and a general process account of imitation. The experiments carried out by the authors of GOADI provide the best evidence in favour of the idea that goals guide imitative performance. Furthermore, mGOADI provides the most clear and well-specified theory highlighting the intrinsic role of mentalistic goals in imitation. Therefore, the experiments carried out in this chapter used manipulations of the pen-and-cups task, a paradigm commonly used to support the view that goals are intrinsic to imitation.

Two tasks were used in Experiment 2.1; one where participants were required to imitate actions carried out by a human model, and one where participants were required to carry out actions in response to moving geometric shapes. Therefore participants either responded to naturalistic or geometric stimuli. Likewise, there were two tasks in Experiment 2.2; one where participants were required to perform actions in response to static geometric shapes and one where participants were required to make verbal responses to static geometric shapes. Therefore, participants either carried out movement or verbal responses. Furthermore, in these experiments, the colouring of the stimuli was altered, such that, in some conditions the hand or grip was differentially coloured instead of the cup. Through these manipulations, I investigated the robustness of the colour minimum error pattern previously observed by Bird et al. and sought to distinguish the predictions of mGOADI from those of a general process account. The specific rationale for each experiment is given below.

Experiment 2.1

In Experiment 2.1, participants either carried out a naturalistic or a geometric version of the pen-and-cups task. In both tasks, participants were required to grasp a pen using either their left or right hand, with a thumbs-up or thumbs-down grip, and to place the

pen into one of two cups. In the naturalistic version, participants were required to copy actions carried out by a human model. In the geometric task, participants were required to respond to moving, abstract, geometric shapes. Each participant carried out two conditions of the experiment; one where the cups were differentially coloured (one red and one blue) and one where the hands were differentially coloured (one red and one blue). In these tasks, error patterns were recorded to investigate the source of the colour minimum error pattern.

If, as suggested by mGOADI, this error pattern is due to inferences about the model's intended goals, then the colour minimum error pattern should not be observed in a task where participants are required to respond to inanimate geometric stimuli. In this task, there is no human model from which to infer intentions, instead, geometric shapes specify which movement to make. Abstract geometric shapes are unlikely to support the attribution of intentions. Therefore, one would not expect to observe the colour minimum error pattern when participants are responding to geometric stimuli.

However, under the general processes account, the colour minimum error pattern is due to general processes. These processes influence a range of tasks and do not rely on attribution of intentions. Therefore, under this view, the colour minimum error pattern should be present in both naturalistic and geometric conditions. That is, in both the naturalistic and geometric task, when the cups are differentially coloured, cup selection should be the most accurate component, and when the hands are differentially coloured, hand selection should be the most accurate component.

2.1.1 Method

Participants. Twenty-four consenting, healthy participants with an average age of 22.5 years, 13 male, were recruited from the UCL Department of Psychology database and paid a small honorarium for their participation. All were right-handed, had normal or correct-to-normal vision, and were proficient in the English language. They were naïve with respect to the purpose of the experiment. Participants were randomly assigned to two groups; naturalistic and geometric. Each participant was tested under both conditions (hands-coloured and cups-coloured) in a counterbalanced order. One participant who did not make any errors was replaced. This experiment, and all experiments reported in this thesis, was performed with local ethical committee approval and in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Stimuli and apparatus. Participants were required to respond to stimuli by performing an action involving grasping a pen and inserting it into one of two cups. Factorial combination of the three components (cup, hand and grip) resulted in 8 possible responses. Participants could make a response using either their left or right hand, to make a thumbs-up or thumbs-down grip, to place the pen into one of the two cups.

Participants in the naturalistic group responded to videos of a model carrying out the actions. For participants in the geometric group the correct response on each trial was indicated by a short stimulus animation. In these animations, the hands were replaced by squares, the grips by short rectangles attached to the squares, and the cups by ellipses.

The geometric shapes were matched to the naturalistic videos in terms of their spatial and temporal characteristics. Each geometric shape was approximately the same size as the corresponding component in the naturalistic videos. Topographical spatial locations of the shapes were equivalent to spatial locations in the naturalistic stimuli. Each shape moved for approximately the same amount of time and with similar trajectory to the corresponding naturalistic component. Figure 1 below depicts the starting positions of the stimuli in the naturalistic condition (1a & 1b) and the geometric condition (1c & 1d).

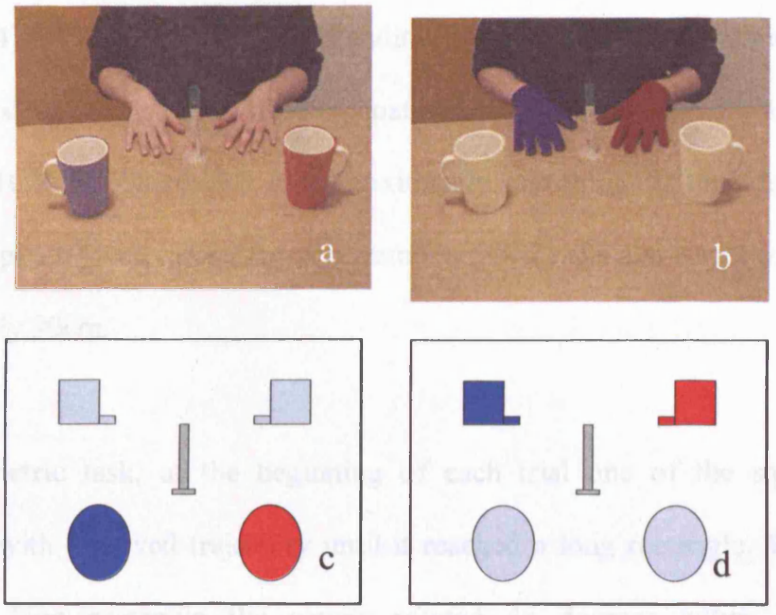


Figure 1: Experiment 2.1.Images depicting the starting position of the stimuli for a) the cups-coloured; b) the hands-coloured condition in the naturalistic task; c) the cups-coloured; and d) the hands-coloured condition in the geometric task.

In the naturalistic task, each video stimulus showed the hands, arms and torso of an adult female as she performed an action sequence. At the beginning of the action sequence, the pen stood upright on a black marker that was fixed to the table. The model grasped the pen using either their left or right hand, with a thumbs-up or thumbs-down grip, to place the pen into one of two cups. Following these movements, the model carried out the actions described above in reverse to return the pen to the black marker. As in previous studies, in the cups-coloured condition, participants saw

the model performing with ungloved hands, and directing her movements to one red cup and one blue cup. The model in the hands-coloured condition wore a red glove on their left hand, and a blue glove on their right hand. The cups presented in the hands-coloured condition were both a light beige, flesh-like colour.

The mean duration of action sequences was 4660ms (SEM = 128.0) for the cups-coloured condition and 4650ms (SEM = 45.0) for the hands-coloured condition. The mean ITI was 1250ms (SEM = 37.5) for the cups-coloured condition, and 1213ms (SEM = 36.4) for the hands-coloured condition. Video stimuli were digitally recorded and presented in colour on an IBM compatible laptop computer with a 38cm screen (resolution 1024 X 678 pixels), at approximately one third of life size. Video clips (720 X 576 pixels) were presented at a frame rate of 25 fps and a viewing distance of approximately 90cm.

In the geometric task, at the beginning of each trial one of the squares moved downwards with a curved trajectory until it reached a long rectangle. While moving toward the long rectangle the square rotated 45 degrees either clockwise or anticlockwise so that the short rectangle attached to it either pointed upwards to the top of the screen (i.e. was positioned on the top of the square) or downwards to the bottom of the screen (i.e. was positioned on the bottom of the square) as it reached the long rectangle. After it had reached the rectangle, both the long rectangle and square moved downwards together with a curved trajectory to one of the ellipses. While moving towards the ellipse, the objects rotated 90 degrees either clockwise or anticlockwise so that the long rectangle, and the direction in which the small rectangle was pointing (up or down), were inverted when they reached the ellipse. Once the objects had reached the ellipse they paused momentarily and then followed the above steps in reverse until

they had reached their starting state. The reverse movements were the equivalent of those used by the human model in the naturalistic task to replace the pen on the black marker.

In the cups-coloured condition the squares (and small rectangles attached to them) were a neutral off-white colour and the ellipses were coloured, one red and one blue. In the hands-coloured condition the ellipses were a neutral off-white colour and the squares (and small rectangles attached to them) were coloured, one red and one blue. In all conditions the blue component was on the left hand side of the stimulus set and the red component was on the right. The mean duration of each action sequence, from shape movement onset until the shapes returned to their initial configuration, was 4500ms (SEM = 165.0) and the ITI was 1100ms (SEM = 39.8). The animation stimuli were presented in colour on an IBM compatible laptop computer with a 38 cm screen (resolution 1024 X 678 pixels), at a viewing distance of approximately 90cm.

To make their responses participants sat at a table upon which was placed a pen and two cups, in the same spatial configuration as used in previous versions of the pen-and-cups task. Figure 2 depicts the spatial relationships between the objects and the effectors at the beginning of a trial in the naturalistic condition.

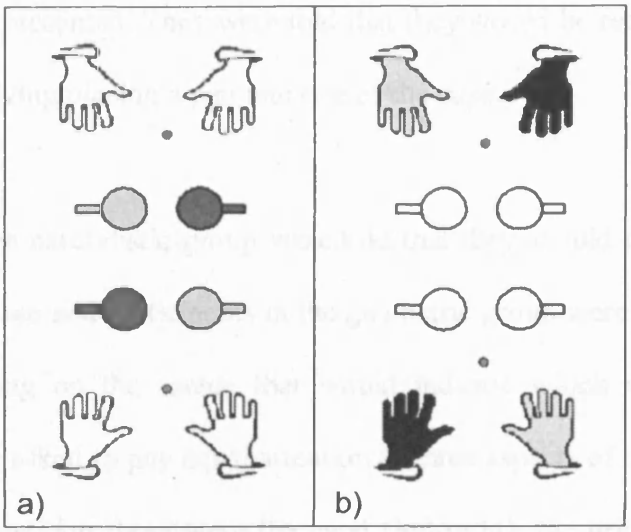


Figure 2: Experiment 2.1. Diagrams indicating the spatial relationships between the model's and observer's objects and effectors at the beginning of each trial for a) the cups-coloured condition and b) the hands-coloured condition in the naturalistic condition. The small dark circles represent pen locations. The larger circles represent cups with handles. There were equivalent spatial relationships between the shape stimuli and the response objects and effectors in the geometric condition.

The cups were placed 35cm from the front of the participant's body, 30cm apart, and equidistant from the participant's midline. At the beginning of each trial, the pen was placed on a marker, a black dot, directly in front of the participant and 23cm from their body. Each cup was 8cm in diameter and 10cm high. The pens (1.5cm diameter, 14cm high) were white with green caps. A transparent plastic disk, 4.8cm in diameter, was attached to the base of each pen to increase its stability when at rest in the upright position. In the cups-coloured condition one cup was blue and one red. In the hands-coloured condition subjects wore a red glove on their left hand and a blue glove on their right hand. The cups were both a neutral off-white colour. The red cup or glove was placed on the participant's left hand side and the blue cup or glove on their right hand side.

Procedure. Participants were tested individually in a quiet room. Each sat at a table bearing the object set and, beyond it, the laptop computer on which the stimulus

animations were presented. They were told that they would be required to make some movements involving placing a pen into one of the cups.

Participants in the naturalistic group were told that they should copy the movements shown on the screen and participants in the geometric group were told that they would see shapes moving on the screen that would indicate which movement to make. Participants were asked to pay equal attention to three aspects of their response: In the cups-coloured condition these were the hand (left/right), the grip (up/down) and the cup (red/blue) and in the hands-coloured condition these were the hand (red/blue), the grip (up/down) and the cup (left/right).

More specifically, the instructions for those in the naturalistic group were as follows: the cups-coloured group was instructed 1) to use their left hand when the model used her left hand, and to use their right hand when the model used her right hand; 2) to grip the pen in the same thumb up or thumb down configuration as the model; and 3) to place the pen in the cup of the same colour as the model. The hands-coloured group was instructed 1) to use their red-coloured hand when the model used her red-coloured hand, and to use their blue-coloured hand when the model used her blue-coloured hand; 2) to grip the pen in the same thumb up or thumb down configuration as the model; and 3) to place the pen in the cup on their left when the model placed the pen in the cup on her left, and to place the pen in the cup on their right when the model placed the pen in the cup on her right.

Instructions for those in the geometric group were as follows: in the cups-coloured condition, participants were instructed 1) to use their left hand when the square on the right moved, and to use their right hand when the square on the left moved; 2) to grip

the pen in the thumbs up position when the small rectangle was positioned on the top of the square and to use the thumbs down position when the small rectangle was positioned on the bottom of the square; and 3) to place the pen in the red cup when the objects moved to the red ellipse and in the blue cup when the objects moved to the blue ellipse. In the hands-coloured condition participants were instructed 1) to use their red hand when the red square moved, and to use their blue hand when the blue square moved; 2) to grip the pen in the thumbs up position when the small rectangle was positioned on the top of the square and to use the thumbs down position when the small rectangle was positioned on the bottom of the square; and 3) to place the pen in the cup on their left when the objects moved to the ellipse on the right of the screen and in the cup on their right when the objects moved to the ellipse on the left of the screen.

Thus, in both tasks participants' responses were spatially incompatible with the movements of the stimuli. For example, in the naturalistic task, if the model used their left hand, which was located on the right hand side of the screen, participants were required to use their spatially incompatible left hand. Similarly, in the geometric condition if the shape on the right moved, participants were required to use their spatially incompatible left hand. Spatially incompatible stimulus-response mappings were used here, as in some previous pen-and-cups experiments (Bird et al., in 2007; Wohlschläger & Bekkering, 2002), because this arrangement yields more errors, and therefore reduces the risk of ceiling effects in this task (Avikainen et al., 2003).

Each participant completed 10 practice trials followed by 80 test trials in each of the two conditions. The test trials comprised 10 presentations of each of the eight action sequences in the cups-coloured or the hands-coloured set, in random order.

Performance was videotaped and the experimenter recorded, for each trial, which hand, grip and cup had been selected by the participant. An error was recorded if the participant selected the incorrect hand or cup or used the incorrect grip as specified by the instructions. Thus, there were three types of errors, relating to the hand, grip and cup components of the task.

2.1.2 Results and discussion

The percentage error score for each component (cup, hand and grip) in each condition was calculated by dividing the number of errors made when responding to the target component in the target condition by the total number of errors made across all components in both conditions. For example, percentage cup error was calculated by dividing the number of trials on which the participant selected the wrong cup by the total number of cup, hand and grip errors made by that participant across all trials in both conditions.

As indicated in Figure 3, similar error patterns were observed for both the naturalistic and geometric tasks. In the cups-coloured condition participants showed the cup<hand<grip error pattern, while errors in the hands-coloured condition followed a different pattern, with the frequencies of cup and grip errors both exceeding the frequency of hand errors. Thus, a colour minimum error pattern was observed in both the naturalistic and geometric tasks.

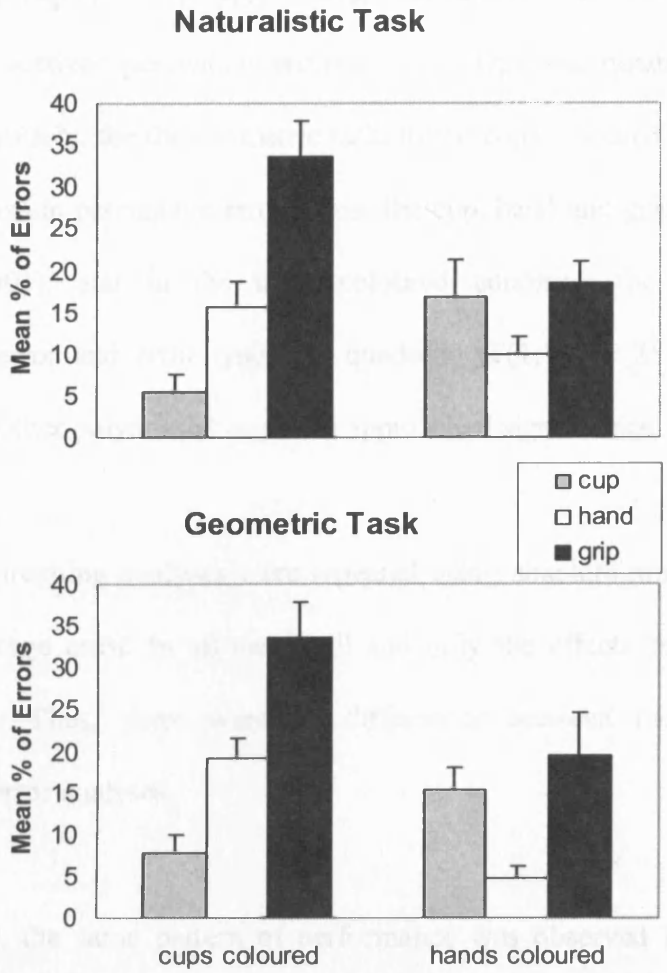


Figure 3: Experiment 2.1. Mean percentage of errors in the naturalistic and geometric versions of the task. Grey bars represent errors on the cup component, white bars represent errors on the hand component and black bars represent errors on the grip component. Vertical bars indicate the standard error of the mean.

Analysis of Variance (ANOVA) with colour (cups-coloured, hands-coloured), and error type (cup, hand, grip) as within-subjects factors and task (naturalistic, geometric) as a between-subjects factor revealed significant main effects of colour ($F(2,22) = 6.80$, $p=.016$), error type ($F(2,22) = 19.78$, $p<.001$), and a significant colour x error type interaction ($F(2,22) = 13.11$, $p<.000$). There were no significant effects or interactions involving the task variable ($F < 1$). Within-subjects contrasts, applied separately to the data from each condition, indicated that for the naturalistic task, in the cups-coloured condition there was a linear increase in percentage error across the cup, hand and grip

categories ($F(1,11) = 33.11$, $p<.001$), and in the hands-coloured condition the relationship between percentage error and error type was quadratic ($F(1,11) = 11.77$, $p=.006$). Similarly, for the geometric task, in the cups-coloured condition, there was a linear increase in percentage error across the cup, hand and grip categories ($F(1,11) = 18.60$, $p=.001$), and in the hands-coloured condition the relationship between percentage error and error type was quadratic ($F(1,11) = 25.62$, $p<.000$). In these analyses no other polynomial contrasts approached significance.

All of the foregoing analyses were repeated using absolute numbers of errors, rather than percentage error. In all cases, all and only the effects reported above reached significance. Thus, there were no differences between the absolute error and percentage error analyses.

In summary, the same pattern of performance was observed in the naturalistic and geometric versions of the task where abstract geometric stimuli, rather than observation of human action, specified the target response. In both tasks a colour minimum error pattern emerged. According to mGOADI, this error pattern is due to inferences about the models intentions. Since the stimuli used in the geometric task were unlikely to support attribution of intentions, mGOADI would not expect a colour minimum error to occur in the geometric task. Therefore, the present results are inconsistent with the predictions made by mGOADI. They are, however, consistent with the general processes account which suggests that the processes that guide imitation are general and are likely to guide a range of tasks. These processes do not rely on the attribution of intentions and should, therefore, be present both when responding to naturalistic human stimuli and geometric stimuli.

Experiment 2.2

In Experiment 2.1, performance did not differ between the naturalistic and geometric version of the task, thus providing evidence inconsistent with the idea that mentalistic goals are necessary for imitative performance.

However, this conclusion rests on the assumption that abstract geometric shapes do not support attribution of intentions and this assumption may not be valid for the stimuli used in Experiment 2.1. It is therefore plausible that performance in the geometric task did not differ from performance in the naturalistic task because participants were attributing intentions to the moving geometric shapes. If this is the case then the results presented in Experiment 2.1 may not be inconsistent with mGOADI.

It has been demonstrated that viewing animated sequences of simple shapes conveys the impression of intentional goal-directed movements in typically developing individuals (Heider & Simmel, 1944). More recent studies investigating theory of mind abilities have shown that participants engage in mentalising when asked to describe the movements of geometric shapes (Castelli, Happé, Frith & Frith, 2002, Castelli, Frith, Happé & Frith, 2000). It has also been demonstrated that the attribution of agency is based on the type of motion or on interaction between objects (Tremoulet & Feldman, 2000; Heider & Simmel, 1944; Scholl & Tremoulet, 2000). Therefore, shapes that do not move and do not interact with each other are less likely to support the attribution of mental states.

In Experiment 2.2, static geometric stimuli were used in order to minimise the possibility that participants would attribute intentions to the shapes. If inferences about mentalistic goals were responsible for the error patterns observed in both conditions in

Experiment 2.1, then one would not expect the same pattern to be observed in Experiment 2.2 because the stimuli used in Experiment 2.2 do not afford the attribution of mentalistic goals. Conversely, if general processes are responsible for the error patterns observed in both conditions in Experiment 2.1, then the same error patterns should be observed in Experiment 2.2: that is, the smallest proportion of errors should be made on the coloured dimension, e.g. fewest cup errors in the cups-coloured condition, and fewest hand errors in the hands-coloured condition.

Experiment 2.2 also contrasted movement responses to the static geometric stimuli, in which participants moved a pen into a cup, with verbal responses to the same stimuli. When responding verbally, participants named the task components, for example, by saying "red" when the red shape flashed, and "blue" when the blue shape flashed. The verbal task was introduced as an additional test of the hypothesis that mentalistic goal processing is an integral component of imitation. Some researchers have suggested that goal processing is an integral component of imitation in the sense that it occurs only, or plays a more important role, when participants are imitating - making isomorphic responses to action stimuli - than when they are responding symbolically or in a non-isomorphic way to action stimuli (e.g. Wohlschläger et al., 2003). If this is correct, then even if participants attribute intentions to the static geometric stimuli in the movement task, they should not do so in the verbal task. Therefore, a colour minimum error pattern in the movement task and not in the verbal task, would suggest that mentalistic goals were attributed to the static geometric stimuli in the movement task, and that this was responsible for the colour minimum error pattern. In contrast, a colour minimum error pattern in both movement and verbal tasks would confirm that this pattern is due to general perceptual and attentional processes, rather than to goal attribution.

Finally, a grips-coloured manipulation was added to Experiment 2.2 to check the generality of the finding, predicted by the general processes account and reported in Experiment 2.1, that the smallest proportion of errors will be made on the coloured component. If this is a general principal, then one would expect, not only minimum cup errors in the cups-coloured condition and minimal hand errors in the hands-coloured condition, but also minimal grip errors in the grips-coloured condition. In order to vary grip colour in a manner analogous to that in which cup and hand colour were varied, the grip variable was changed such that, instead of a thumbs up or thumbs down grip, participants were required to use an inside or outside grip. For an inside grip, participants were required to grip the pen between their index and middle fingers and for the outside grip they held the pen between their ring and little fingers.

2.2.1 Method

Participants. A further 24 consenting, healthy participants with an average age of 22.6 years, 8 male, were recruited from the UCL Department of Psychology database and paid a small honorarium for their participation. All were right-handed, had normal or correct-to-normal vision, and were proficient in the English language. They were naïve with respect to the purpose of the experiment. Participants were randomly assigned to two groups; movement task and verbal task. Each participant was tested under all three conditions (hands-coloured, cups-coloured and grips-coloured) in a counterbalanced order. Two participants, who made no errors during the test trials, were replaced.

Apparatus and stimuli. The apparatus and stimuli were similar to those in the geometric condition of Experiment 2.1 except that the shapes on the screen did not change their positions in the course of each trial. Instead, they flashed to indicate the

correct response. Figure 4 depicts the layout of the new stimuli. The spatial configuration of the objects on the screen and the temporal properties of the flashing were matched to the movements from Experiment 2.1, i.e. each shape flashed for the same amount of time as it had moved in Experiment 2.1.

To enhance grip discriminability, Experiment 2.2 used a new grip manipulation. Instead of being required to perform an up or down grip, participants were required to use an inside or outside grip. For an inside grip the participant held the pen between their index and middle fingers and for the outside grip they held the pen between their ring and little fingers. The new grip manipulation was represented in the stimulus layout by two rectangles attached to the bottom of the square. These indicated the use of either an inside or outside grip.

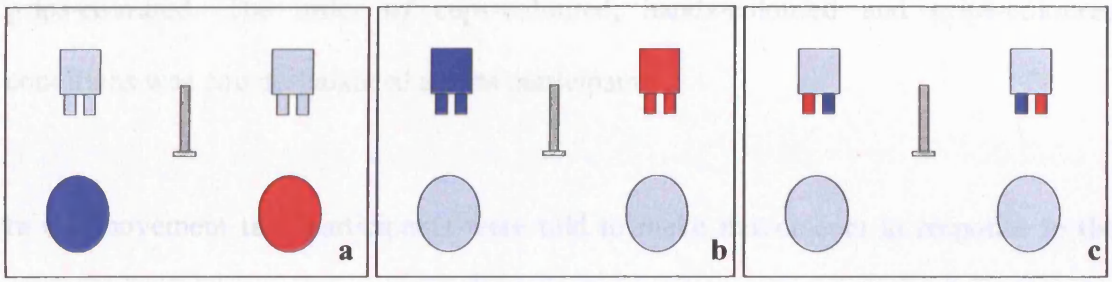


Figure 4: Experiment 2.2. Images depicting the starting position of the stimuli in a) the cups-coloured condition, b) the hands-coloured and c) the grips-coloured condition.

During each trial, consecutive stimulus flashes indicated which action to perform. Initially, one of the squares flashed on and off the screen (specifying which hand was to be used), followed by the long rectangular object (representing the pen) and finally one of the two ellipses (specifying the target cup). While the square flashed, one of the small rectangles attached to the squares disappeared briefly so that only one remained visible (specifying which grip to select). After the ellipse flashed, the shapes then followed the above steps in reverse, finishing with the square flashing. The reverse

flashes were the equivalent of those used by the human model in the naturalistic task to replace the pen on the black marker.

For participants in the movement group, the response apparatus was the same as that used in Experiment 2.1 for the cups-coloured and hands-coloured conditions except that in the grips-coloured condition the participant wore gloves with coloured fingers. The gloves were an off-white neutral colour except for blue index and middle fingers and red ring and little fingers. There was no pen and cup apparatus present for participants in the verbal group.

Procedure. The procedure was the same as in Experiment 2.1 except as follows. Each participant was tested under three conditions: cups-coloured, hands-coloured and grips-coloured. The order of cups-coloured, hands-coloured and grips-coloured conditions was counterbalanced across participants.

In the movement task participants were told to make movements in response to the flashing shapes. More specifically, in the cups-coloured condition the instructions distinguished cups by their colour and distinguished hands and grips using spatial codes. Thus, participants were told 1) to use their left hand when the square on the right flashed, and to use their right hand when the square on the left flashed; 2) to use an inside grip when the rectangle on the inside remained visible or an outside grip when the rectangle on the outside remained visible; and 3) to place the pen in the red cup when the red ellipse flashed and in the blue cup when the blue ellipse flashed.

In the hands-coloured conditions, the instructions distinguished hands by their colour and distinguished hands and grips using spatial codes. Thus, participants were told 1)

to use their red hand when the red square flashed, and to use their blue hand when the blue square flashed; 2) to use an inside grip when the rectangle on the inside remained visible or an outside grip when the rectangle on the outside remained visible; and 3) to place the pen in the cup on the left when the square on the right flashed, and in the cup on the right when the square on the left flashed.

In the grips-coloured conditions, the instructions distinguished grips by their colour and distinguished hands and cups using spatial codes. Thus, participants were told 1) to use their left hand when the square on the right flashed, and to use their right hand when the square on the left flashed; 2) to use their red fingers to grip when the red rectangle remained visible and their blue fingers when the blue rectangle remained visible; and 3) to place the pen in the cup on the left when the square on the right flashed, and to place the pen in the cup on the right when the square on the left flashed.

In the verbal task, participants were required to respond verbally to the flashing shapes. More specifically, in the cups-coloured conditions the instructions distinguished cups by their colour and distinguished hands and grips using spatial codes. Thus, participants were told 1) to say "left", when the square on the right flashed, and to say "right" when the square on the left flashed; 2) to say "inside" when the rectangle on the inside remained visible and "outside" when the rectangle on the outside remained visible; and 3) to say "red" when the red ellipse flashed and "blue" when the blue ellipse flashed.

In the hands-coloured condition, the instructions distinguished hands by their colour and distinguished hands and grips using spatial codes. Thus, participants were told 1) to say "red" when the red square flashed, and to say "blue" when the blue square

flashed; 2) to say "inside" when the rectangle on the inside remained visible and "outside" when the rectangle on the outside remained visible; and 3) to say "left" when the ellipse on the right flashed, and "right" when the ellipse on the left flashed.

In the grips-coloured condition, the instructions distinguished grips by their colour and distinguished hands and cups using spatial codes. Thus, participants were told 1) to say "left" when the square on the right flashed, and to say "right" when the square on the left flashed; 2) to say "red" when the red rectangle remained visible and "blue" when the blue rectangle remained visible; and 3) to say "left" when the ellipse on the right flashed, and "right" when the ellipse on the left flashed.

2.2.2 Results and discussion

As in Experiment 2.1, the percentage error score for each component (cup, hand and grip) in each condition was calculated by dividing the number of errors made when responding to the target component in the target condition by the total number of errors made across all components in both conditions.

As indicated in Figure 5, similar error patterns were observed in the movement and verbal tasks, in that the coloured component was the most accurate component in all three conditions of both tasks. In the cups-coloured condition the frequency of hand and grip errors both exceeded the frequency of cup errors, while errors in the hands-coloured and grips-coloured conditions followed a different pattern. In the hands-coloured condition, the frequencies of cup and grip errors both exceeded the frequency of hand errors, and in the grips-coloured condition the frequency of hand and cup errors both exceeded the frequency of grip errors.

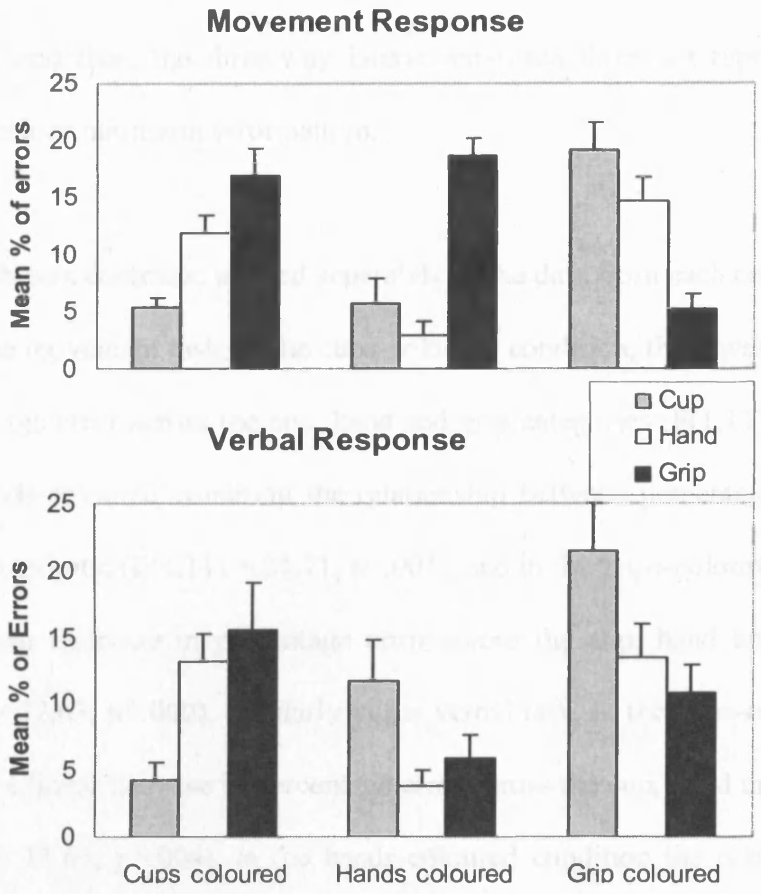


Figure 5: Experiment 2.2. Mean percentage of errors in the movement and verbal response versions of the task. Grey bars represent errors on the cup component, white bars represent errors on the hand component and black bars represent errors on the grip component. Vertical bars indicate the standard error of the mean.

ANOVA was applied to the percentage error scores, with colour (cups-coloured, hands-coloured, grips-coloured), and error type (cup, hand, grip) as within-subjects factors and task (movement, verbal) as a between-subjects factor revealed a significant main effect of colour ($F(2,22) = 4.23$, $p=.021$), a significant coloured x error type interaction ($F(2,22) = 16.712$, $p<.001$) and a significant colour x error type x task interaction ($F(2,22) = 3.98$, $p=.005$). Inspection of the means suggests that the three-way interaction was due to different proportions of cup and grip errors, across tasks, in the hands-coloured condition. This may reflect the difference in difficulty between identification and execution of the grip component. Importantly, however, in both tasks, the hand represents the most accurate component in the hands-coloured

condition, and thus, the three-way interaction result does not represent a departure from the colour minimum error pattern.

Within-subjects contrasts, applied separately to the data from each condition, indicated that for the movement task, in the cups-coloured condition, there was a linear increase in percentage error across the cup, hand and grip categories ($F(1,11) = 2.64$, $p=.018$), in the hands-coloured condition the relationship between percentage error and error type was quadratic ($F(1,11) = 21.71$, $p=.001$), and in the grips-coloured condition there was a linear decrease in percentage error across the cup, hand and grip categories ($F(1,11) = 37.63$, $p<.000$). Similarly in the verbal task, in the cups-coloured condition there was a linear increase in percentage error across the cup, hand and grip categories ($F(1,11) = 13.63$, $p=.004$), in the hands-coloured condition the relationship between percentage error and error type was quadratic ($F(1,11) = 7.75$, $p=.018$), and in the grips-coloured condition there was a linear decrease in percentage error across the cup, hand and grip categories ($F(1,11) = 5.11$, $p=.045$).

As in Experiment 2.1, the foregoing analyses were repeated using absolute errors as opposed to the percentage error score described above. In these analyses, all and only the effects reported above reached significance. Thus, there were no differences between the absolute error and percentage error analyses.

In summary: in this experiment where participants responded to static geometric stimuli, similar patterns of performance were observed both in the movement and verbal versions of the task such that the coloured component always represented the most accurate component. These findings are not consistent with the idea that

mentalistic goals guide performance but rather suggest that general processes guide performance on this task.

2.3 General discussion

Several accounts of imitation suggest that actions are coded in terms of goals, and that these goals are used to translate sensory representations into matching motor outputs (e.g. AIM, Meltzoff & Moore, 1997; GOADI, Wohlschläger et al., 2003). The goal-directed theory of imitation (GOADI) provides the most explicit statement of this view. In one version of this theory, goals are presumed to be action outcomes. Support for this position was provided by the well-replicated finding that, in the pen-and-cups task, participants imitate object selection more accurately than effector selection, which is imitated more accurately then grip selection. This is manifested in the pen-and-cups task as a cup<hand<grip error pattern. However, an alternative explanation was presented by Bird et al. (in press), who argued that this error pattern was due to more general processes, specifically stimulus discriminability. They found that when the colour cue was moved from the cups to the hands or the grips, these components became the most accurately imitated components of the action, thus demonstrating a colour minimum error pattern. Such a pattern of errors is clearly inconsistent with GOADI's claim of a strict hierarchy of action goals where objects and their treatments are always imitated more accurately than the means used to achieve those goals.

However, the mentalistic version of GOADI (mGOADI) is compatible with the results of Bird et al. (2007). Under mGOADI, goals are not defined as observable action end-states, but rather as inferred mental states of the model. Therefore, the effect of the colour cue in the experiments reported by Bird et al., may have been to alter which action component was inferred by the participant to be the goal of the movement.

To test mGOADI against a general processes account, in Experiments 2.1 and 2.2 participants responded to abstract geometric shapes, which are unlikely to support the attribution of mental states. In Experiment 2.1, participants were either required to respond to naturalistic stimuli or moving geometric stimuli. If the colour minimum error pattern was due to inference of mental state goals, this pattern should not have been present in this non-mentalistic version of the task. Contrary to this prediction, the colour minimum error pattern was found both when participants were required to make movements in response to naturalistic and to geometric stimuli. In Experiment 2.2, static geometric shapes were used as stimuli to further reduce the possibility that participants attributed intentions to the shapes. Furthermore, in this task, participants either carried out movements or responded verbally. The colour minimum error pattern was observed both in the movement and verbal versions of the task. This observation of the colour minimum error pattern in both tasks where responses were made to static stimuli provides evidence against mGOADI. Furthermore, the observation of this error pattern in the verbal task which contains no action stimuli or action responses provides further evidence inconsistent with the idea that mentalistic goals are responsible for this error pattern. The current results are consistent with the idea that general processes guide performance, since these processes are thought to influence a range of tasks and do not rely on inferences about mental states. These results imply that the coloured components represented the most accurate component because colour enhanced discriminability or drew attention to that particular component of the stimulus sequence.

It has been suggested that error patterns in tasks, like the pen-and-cups task, provide support for the view that goals guide imitation. However, the results of the present study suggest that, contrary to this hypothesis, it is not necessary to invoke goal

processing to explain imitation performance on this task. Consequently, the error patterns seen in the pen-and-cups task do not provide specific support for goal-directed theories. Thus, the results from this chapter challenge evidence put forward to support the claims of specialist theories.

The results from this chapter are consistent with a general process account which supposes that imitation is guided by general processes that influence a range of tasks rather than any processes specific to imitation. They are therefore consistent with both generalist theories described in this thesis. Both ASL and IM suggest that sensory and motor representations become linked with no intermediate goal processing stage. Accordingly, goals are not necessary to solve the correspondence problem. Thus, these theories imply that there is no special relationship between goals and imitation. However, neither generalist theory explicitly denies that goal processing and intention reading may sometimes be involved in the performance of imitative tasks, as they are involved in the performance of non-imitative tasks. Introspection leaves little doubt that many of our imitative actions are guided by goals and intentions; we commonly perform imitative and non-imitative actions with some purpose in mind. However, simply because goals play a role in our imitative behaviour does not imply that they are a necessary component of imitation or that they play a role in solving the correspondence problem. Therefore, it is not necessary to evoke goals in order to explain *how* we imitate. Inferring the intentions of another or understanding the expected outcome of a certain action might, on some occasions, help to explain *why* I did the same thing as a model, but it does not explain *how* I was able to do it. Consequently, goals are more likely in inform *what* we imitate and not *how* we imitate.

Chapter 3: Intentional imitation in individuals with ASD:

Observed imitation impairments in ASD can be explained by non-specific factors

The aim of the following two chapters is to investigate imitative abilities in individuals with ASD in order to ascertain whether an imitation-specific impairment exists in ASD. Accordingly, Chapters 3 and 4 examine another line of evidence that has been suggested to support a specialist view of imitation.

Imitation has been extensively studied in ASD (e.g. Williams et al., 2004). The majority of studies have reported poor performance in imitation tasks, and therefore, the general consensus is of an imitation impairment in ASD (Williams et al., 2004). However, despite the wealth of studies, some are contradictory; not all studies have found an impairment (e.g. D'Entremont & Yazbek, in press; Hamilton et al., 2007).

Imitation is relevant to theories of ASD, because it has been suggested to underpin the development of social cognition, including theory of mind, empathy, and the development of language (Rogers & Pennington, 1991). Impairments in these abilities characterise individuals with ASD, which has prompted some theorists to suggest that an imitation impairment is the core deficit in ASD (Williams et al., 2001).

Additionally, ASD is relevant to theories of imitation. The existence of an imitation impairment in ASD would appear to be consistent with the idea that imitation is mediated by a special-purpose mechanism, since such a mechanism should be susceptible to selective impairment, that is, an impairment in one domain that is not associated with more generalised deficits (Fodor, 1983).

It is, therefore, important to make sense of the conflicted findings in the literature and to establish whether there is compelling evidence for an imitation impairment in ASD. In order to do this, it is necessary to explore possible explanations for the conflicting findings.

Mixed findings may reflect the substantial heterogeneity within the autism spectrum; it is possible that some individuals with ASD have an imitation impairment while others do not. Repeated sampling of this heterogeneous population with the relatively small number of participants typically used in studies of imitation would lead to some studies demonstrating imitation impairments in ASD and some not.

An alternative source of the variance in imitation performance across studies may be the types of tests used to measure imitation. The majority of tasks used to date have been complex intentional imitation tasks. These tasks require a number of abilities in addition to imitation: the understanding of social cues and language to judge when imitation is required and what dimensions of action are to be imitated; theory of mind to understand the pretence and intention behind pantomimed transitive actions; executive functions to organise and interpret sequences of actions correctly; effective perceptual processing to perceive complex moving stimuli, and motor control to carry out observed movements. All of these abilities may be taxed to a greater or lesser extent in the experimental tasks used to study imitation.

Understanding social cues, language, theory of mind, executive functions, perceptual and motor skills are not imitation-specific abilities. They are necessary for a large number of imitative and non-imitative tasks. Thus, poor performance on tests of imitation due to problems with these non-specific abilities would not constitute an

imitation-specific impairment. As highlighted throughout this thesis, there is one problem unique to imitation: motor output must be produced which matches perceptual input. Two seemingly incommensurate codes, one relating to patterns of stimulation received through the distal senses and the other to muscle activations, must be made commensurate (the 'correspondence problem', Heyes, 2001). The ability to solve this problem, i.e. to translate perceptual representations of action into motor commands, is, therefore, the key test of imitation. If imitation represents the core deficit in ASD, it is this mechanism that is disturbed.

Thus, there are two possible explanations for the mixed findings in the ASD imitation literature. First, there is an imitation-specific impairment in ASD; that is the mechanism by which motor outputs are matched to perceptual input is in some way disturbed. Second, there is no specific imitative impairment in ASD. Rather, poor performance on tests of imitation is due to impairments of non-specific mechanisms - such as theory of mind, executive function - which are required for successful performance on these tests. The current chapter sought to distinguish these two possibilities by investigating whether observed impairments in imitative performance can be accounted for by more general abilities not specific to imitation.

A group of high functioning adults with ASD was compared to a matched typically developing control group on an intentional imitation task. The pen-and-cups task was used because individuals with ASD have been shown to make more errors than controls on this task (Avikainen et al., 2003). As described in Chapter 2, this task is demanding because, in order to minimise errors, the participant needs to keep track of three dimensions of action: object selection, effector selection and grip selection.

Experiment 3.1 replicated the finding (Avikainen et al., 2003) that individuals with ASD make more errors in the pen-and-cups tasks. Experiment 3.2 sought to establish whether this finding reflects an imitation-specific impairment, or instead an impairment in non-specific mechanisms. In Experiment 3.2, participants completed two non-imitative versions of the pen-and-cups task which dissociated the components of the imitative stimulus-response relationship involved in the original pen-and-cups task. In the original version, action responses are made to action stimuli. In Experiment 3.2, one task involved action responses being made to abstract geometric stimuli, while the other required participants to describe verbally the original action stimuli. Thus, the action stimulus and action response components were separately removed while all other aspects of the task were held constant. Since neither of the tasks in Experiment 3.2 involved making a matching action in response to an observed action, neither of these tasks could be described as an imitative task. Therefore, if the impaired performance on the pen-and-cups task in ASD is due to an imitation-specific impairment, one would expect improved performance on these, non-imitative, versions of the task. Alternatively, if the impaired performance on the pen-and-cups task is due to non-specific mechanisms, then similarly impaired performance is also expected on the non-imitative versions of the task.

Experiment 3.1

The aim of Experiment 3.1 was to establish whether the current sample of individuals with ASD demonstrated impaired performance in a test of intentional imitation. If this is the case, then the specificity of this deficit could be tested in Experiment 3.2. Accordingly, Experiment 3.1 sought to replicate the finding of impaired imitation on the pen-and-cups task by individuals with ASD reported by Avikainen et al. (2003). In this experiment, two conditions were completed by participants. Both were imitative,

but the two conditions differed in terms of their imitative frame of reference. In the 'mirror' condition, participants were asked to imitate as if in a mirror; that is they were to imitate an action completed by the model's right hand with their spatially compatible left hand, and vice versa. Similarly, if the pen was placed into the cup on the model's right side, then the participant was to place their pen in the spatially compatible cup which was on the participant's left side. Conversely, the 'transpose' condition required participants to use an anatomical frame of reference; actions completed by the model with their right hand should be imitated with the participants own right hand. Similarly, if the pen was placed in the cup on the right side of the model, the participant must place their pen in the cup on their own right side (see Figure 1). Avikainen et al. found that although the control group showed better performance when required to mirror imitate (in comparison with the transpose condition), the ASD group showed no such improvement. The secondary aim of Experiment 3.1 was, therefore, to establish whether this effect of condition could be replicated.

The experiment was performed as by Avikainen et al. with one exception; video recordings of the actions (rather than a live demonstrator performing the actions) were presented to increase stimulus control. Use of video stimuli allows the interval between actions and their durations to be standardized across conditions and groups, and it has previously been shown that presenting video stimuli does not alter either the error rate or error pattern on the pen-and-cups task (Bird et al., in press).

As highlighted in Chapter 2, a particular error pattern typically emerges in the pen-and-cups task. Adults usually make fewer cup errors than hand errors and fewer hand errors than grip errors (Avikainen et al., 2003, Wohlschläger & Bekkering 2002). This

cup<hand<grip error pattern has been suggested to reflect the importance of goals, and in particular mentalistic goals, in imitation (Gattis et al., 2002). Given the widely reported deficits in mentalising in ASD (e.g. Baron-Cohen et al., 1985; Frith & Frith, 2003), on the basis of specialist claims that this error pattern is due to mentalistic goal attribution, one may expect a different error pattern to emerge in individuals with ASD. However, the findings from the previous chapter and from Bird et al. (2007) imply that general perceptual and attentional processes, rather than goals, drive this error pattern. If this is the case then one may not expect individuals with ASD to be any less susceptible to these cues than typically developing individuals and one should, therefore, expect them to show a similar cup<hand<grip error pattern. Consequently, a demonstration of this error pattern in the ASD group in the current experiment would be consistent with the findings in the previous chapter.

Finally, the cup<hand<grip error pattern indicates that the participant is carrying out the task correctly; for example, if a participant only attends to two components of the task, different error patterns may emerge. It is important to demonstrate that individuals with ASD are engaging in the task and following task instructions properly to ensure that any poor performance is not purely motivational or due to a failure to understand task instructions. Therefore, if individuals with ASD demonstrate the typical cup<hand<grip error pattern this will imply that they are carrying out the task correctly and any group differences are more likely to be interpretable.

3.1.1 Methods

Participants. Thirty-two individuals participated in the study: 16 participants with autism spectrum disorder (14 male; 2 female) and 16 typically developing control participants (14 male; 2 female). Participants were recruited from the UCL, Institute of

Cognitive Neuroscience database. The groups were matched on gender, age (ASD M: 37 years SEM: 3.4, control M: 35 years, SEM: 3.7), and IQ (ASD FSIQ M: 119, SEM: 3, VIQ M: 117, SEM: 3, PIQ M: 116, SEM: 4 Control FSIQ M 118, SEM: 3, VIQ M: 117, SEM: 3, PIQ M: 112, SEM: 2). IQ was measured using the Wechsler Adult Intelligence Scale-3rd UK Edition (Wechsler, 1999). All participants in the ASD group had previously received a diagnosis from an independent clinician according to standard criteria. The autism diagnostic observational schedule – Generic (ADOS-G, Lord et al., 2000), was used in order to characterize the participants. On this measure ten participants met criteria for autism, while six participants met criteria for autism spectrum disorder. All participants were right-handed, had normal or corrected-to-normal vision and were naive with respect to the purpose of the experiment.

Stimuli and apparatus. Stimuli and apparatus were identical to the naturalistic task in experiment 2.1 except as follows: The spatial relationship of the model's and participant's cups varied according to condition. In the mirror condition the cups were arranged so that they were spatially compatible from the participant's perspective, i.e. both the participant's and the model's blue cup was on the participants' left side (see Figure 6b). In the transpose condition the cups were arranged so that they were spatially incompatible from the participant's perspective (i.e. the participant's blue cup was on their left side but the model's blue cup was on the participant's right side, see Figure 6a).

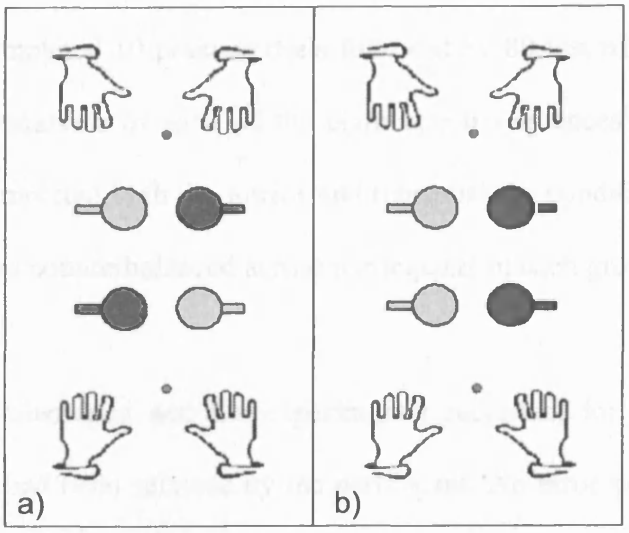


Figure 6: Experiment 3.1. Diagrams indicating the spatial relationships between the model's and observer's objects and effectors at the beginning of each trial for a) the transpose condition and b) the mirror condition

Procedure. Participants were tested individually in a quiet room. Each sat at a table bearing the object set and, beyond it, the laptop computer on which the video stimuli were presented. They were told that they would be shown a video and that, while watching it, they should imitate the movement sequences as simultaneously as possible, paying equal attention to three aspects: the hand (left/right), the grip (up/down) and the cup (red/blue). Specific instructions varied according to condition. In the transpose condition participants were instructed 1) to use their left hand when the model used her left hand, and to use their right hand when the model used her right hand; 2) to grip the pen in the same thumb up or thumb down configuration as the model; and 3) to place the pen in the cup of the same colour as the model. In the mirror condition participants were instructed 1) to use their left hand when the model used her right hand, and to use their right hand when the model used her left hand; 2) to grip the pen in the same thumb up or thumb down configuration as the model; and 3) to place the pen in the cup of the same colour as the model. After giving the instructions, the experimenter demonstrated the correct response in each condition until the participants reported that they understood the task.

Each participant completed 10 practice trials followed by 80 test trials. The test trials comprised 10 presentations of each of the eight action sequences in random order. Each participant completed both the mirror and transposition conditions and the order of the conditions was counterbalanced across participants in each group.

Performance was videotaped and the experimenter recorded, for each trial, which hand, grip and cup had been selected by the participant. An error was recorded if the participant's selection did not match that of the model as specified in the instructions. Thus, there were three types of errors, relating to the hand, grip and cup components of the task, respectively. These were summed for each participant to give a total error score. Absolute numbers of errors were used, instead of the percentage measure used in the previous chapter, so that direct comparisons of imitative performance could be made across groups.

3.1.2 Results and discussion

The mean total number of errors made by each group in both the mirror and transpose conditions is shown in Figure 7.

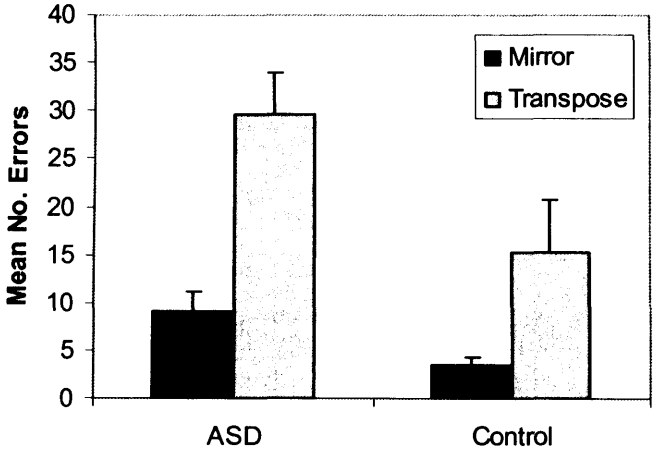


Figure 7: Experiment 3.1 Mean number of errors (out of a possible 240) made by the ASD and control groups in both the mirror (black bars) and transpose (grey bars) conditions in the imitative version of the task. Vertical bars indicate the standard error of the mean.

These data were entered into an ANOVA with a within-subjects factor of condition (transpose and mirror), and a between-subjects factor of group (ASD and control). The main effect of group was significant ($F(1,30) = 5.7$, $p = 0.023$), indicating that the ASD group made significantly more errors than the control group. The main effect of condition was also significant ($F(1,30) = 25.3$, $p<0.001$), revealing that the transpose condition was more challenging than the mirror condition. The interaction between condition and group was not significant ($F(1,30) = 1.9$, $p=0.183$) indicating that the degree of impairment shown by the ASD group, relative to the control group, did not vary as a function of task condition. Simple effects analyses were used to test whether the groups' performance differed significantly in each of the conditions. This analysis confirmed that the performance of the ASD group was significantly less accurate than that of the controls in both the transpose ($F(1,30) = 4.2$, $p=0.049$) and the mirror ($F(1,30) = 4.7$, $p=0.038$) conditions.

Both groups showed the usual cup<hand<grip error pattern (as shown in Table 1 below) in both mirror and transpose conditions, as tested using linear contrasts (ASD mirror: $F(1,15) = 14.1$ $p=0.002$ ASD transpose: $F(1,15) = 44.3$ $p<0.001$ control mirror: $F(1,15) = 18.7$ $p = 0.001$ control transpose: $F(1,15) = 8.5$ $p = 0.011$).

ASD						Control					
Mirror			Transpose			Mirror			Transpose		
Cup	Hand	Grip	Cup	Hand	Grip	Cup	Hand	Grip	Cup	Hand	Grip
0.38	2.75	6.06	2.38	9.94	17.38	0.38	0.63	2.63	2.38	4.88	8.13
0.15	1.44	1.42	0.57	2.24	2.28	0.20	0.30	0.45	1.39	1.92	2.39

Table 1: Experiment 3.1. Mean (and standard error of the mean) number of cup, hand and grip errors in Experiment 3.1 for the ASD and control Groups.

The primary purpose of Experiment 3.1 was to establish whether the particular sample of adults with ASD who took part in this study showed an impairment on both the mirror and transpose conditions of the pen-and-cups task. The results clearly show that the ASD group made more errors than the control group in both conditions.

The secondary purpose of Experiment 3.1 was to examine the pattern of performance in mirror and transpose conditions in both groups. Avikainen et al. (2003) reported that, in contrast to the control group, individuals with ASD did not show better performance in their imitation performance when required to mirror imitate. Such a pattern of results would have been manifested in Experiment 3.1 by a significant interaction between the condition and group factors, indicating that the difference in performance between the groups depended on whether imitating in a mirror or transposition fashion. However, this interaction was not significant. Indeed, the ASD group tended to show a greater impairment on the transpose condition, and therefore, the finding of a selective impairment in mirror imitation in ASD was not replicated.

Finally the cup<hand<grip error pattern, that is typically shown by participants on this task, was observed in this experiment. This is consistent with the findings from Chapter 2, as it implies that this error pattern does not rely on mentalising skills, and also confirms that the participants were following task instructions correctly.

Experiment 3.2

Experiment 3.1 demonstrated impaired performance on the pen-and-cups intentional imitation task by a group of adults with ASD. Experiment 3.2 aimed to identify whether the poor performance observed in Experiment 3.1 was due to a deficit in an imitation-specific mechanism which translates observed actions into motor output, or

whether the poor performance was due to non-specific mechanisms which are necessary for accurate task performance but which are not specific to imitation.

The same participants who had completed Experiment 3.1 were asked to complete two versions of the pen-and-cups task which did not require imitation, but which included the same non-specific task demands as in the original, imitative, pen-and-cups task. In an imitation task, matching action responses are made to action stimuli. In order to remove the requirement to imitate in the pen-and-cups task, the imitative stimulus-response relationship was altered in two alternative versions of the task. In the 'geometric' version of the pen-and-cups task participants were required to make the same action responses as in the imitative version of the task, but in response to the movement of abstract geometric shapes rather than to action stimuli. In the 'verbal' version of the pen-and-cups task, participants observed the same action stimuli as in the imitative version of the task but were asked to describe the sequences rather than to make action responses.

In order to test the specificity of any imitation deficit in ASD the performance of the ASD group in each of the non-imitative versions of the task was compared to their performance in the imitative version of the task. If the impaired performance shown by the ASD group in the imitative version of the task is due to an imitation-specific deficit, then removing the imitative nature of the task should result in improved performance relative to that of the control group. However, if the poor performance of the ASD group in Experiment 3.1 was due to non-specific factors, then one would expect the performance of the ASD group to be as impaired in the alternative versions as in the imitative version of the task. This is because these non-specific task components are preserved in both non-imitative versions.

3.2.1 Method

Participants. Twenty-four of the original thirty-two individuals were able to attend the second testing session, 12 participants with autism spectrum disorder (11 male; 1 female) and 12 typically developing control participants (11 male; 1 female). Groups were matched on gender, age (ASD M: 38 years SEM: 3.3, control M: 37 years, SEM: 3.4), and IQ (ASD FSIQ M: 118, SEM: 4, VIQ M: 117, SEM: 4, PIQ M: 113, SEM: 5 Control FSIQ M 118, SEM: 3, VIQ M: 117, SEM: 3, PIQ M: 110, SEM: 2). Of the 12 participants with ASD who returned for the second session, seven participants met criteria for autism, while five participants met criteria for autism spectrum disorder as measured by the ADOS-G.

Participants completed both the geometric and verbal version of the pen-and-cups task in a second session, which was scheduled between one and four months after the initial testing session.

Stimuli and Apparatus: Geometric Version. Participants made the same responses, using the same apparatus, as in Experiment 3.1. The correct response on each trial was communicated to the participant by presenting a short stimulus animation. These animations were identical to those used in the cups-coloured condition of the geometric task in experiment 2.1 (see Fig. 8).

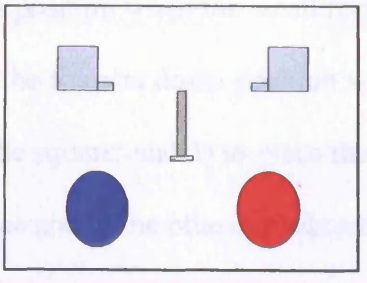


Figure 8: Experiment 3.1. Image depicting the starting position of the animation stimulus specifying the action response to be made by the participants in the geometric version of the task.

The animation stimuli for the mirror and transpose versions were distinguished according to the colouring of the ellipses ('cups'). In the transpose condition the colour of the ellipses and the cups with which participants made their responses was spatially compatible from the participant's perspective. For example, if the participant's red cup was on their left, and the blue cup on their right, then the blue stimulus ellipse was on the left of the screen and the red stimulus ellipse was on the right of the screen. In the mirror condition the location of the stimulus ellipses and the cups was spatially compatible, for example both the blue cup and blue stimulus ellipse was on the left of the screen while the red cup and red ellipse was on the right of the screen.

Procedure: Geometric Version. The procedure was the same as the geometric version of Experiment 2.1 except as follows. In the transpose condition, participants were instructed 1) to use their left hand when the square on the right of the screen moved, and to use their right hand when the square on the left moved; 2) to grip the pen in the thumbs up position when the small rectangle was positioned on the top of the square and to use the thumbs down position when the small rectangle was positioned on the bottom of the square; and 3) to place the pen in the red cup when the objects moved to the red ellipse and in the blue cup when the objects moved to the blue ellipse. In the mirror condition, participants were instructed 1) to use their left hand when the square on the left moved, and to use their right hand when the square on the right moved; 2) to grip the pen in the thumbs up position when the small rectangle was positioned on the top of the square and to use the thumbs down position when the small rectangle was positioned on the bottom of the square; and 3) to place the pen in the red cup when the objects moved to the red ellipse and in the blue cup when the objects moved to the blue ellipse.

Stimuli and Apparatus: Verbal Version. The stimuli were identical to those presented in Experiment 3.1. The participants were not given the object set (cups and pen) because action responses were not required.

Procedure: Verbal Version. The procedure was the same as that of Experiment 3.1 except as follows. All participants were instructed to describe, rather than to imitate, the model's movements. In the mirror condition participants were told 1) to say 'left hand' when the model used her hand on the participant's left, and to say 'right hand' when the model used her hand on the participant's right; 2) to say 'up grip' or 'down grip' according to the orientation of the model's thumb; and 3) to say 'red cup' or 'blue cup' in response to the model's object selection. In the transpose condition participants were instructed 1) to say 'left hand' when the model used her hand on the participant's right, and to say 'right hand' when the model used her hand on the participant's left; 2) to say 'up grip' or 'down grip' according to the orientation of the model's thumb; and 3) to say 'red cup' or 'blue cup' in response to the model's object selection.

3.2.2 Results and discussion

The aim of Experiment 3.2 was to compare the performance of the ASD group, relative to controls, in two non-imitative versions of the task with their performance in the imitative version completed in Experiment 3.1. The mean number of errors made by each group, in each condition, is shown in Figure 9.

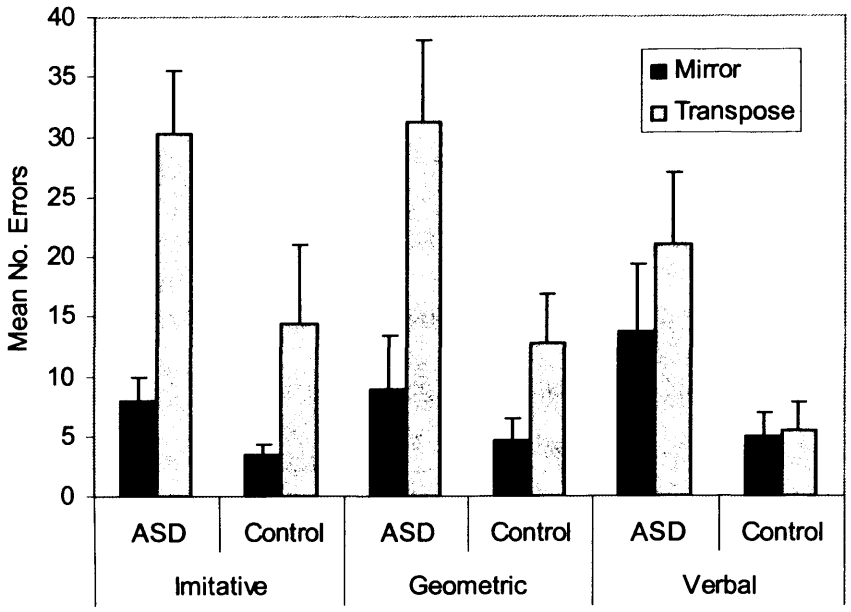


Figure 9: Experiment 3.2. Mean number of errors (out of a possible 240) made by the ASD and control groups in both the mirror (black bars) and transpose (grey bars) conditions in the imitative, geometric and verbal versions of the task. Vertical bars indicate the standard error of the mean.

These data were entered into an ANOVA with within-subjects factors of version (imitative, geometric, and verbal), and condition (mirror and transpose), and a between-subjects factor of group (ASD and control). This analysis revealed a significant main effect of condition ($F(1,22) = 21.5$, $p<.001$), reflecting the increased error rate in the transpose condition, and a significant main effect of group ($F(1,22) = 6.1$, $p=.022$), due to the greater number or errors made by the ASD group. The interaction between condition and group was significant ($F(1,22) = 4.4$, $p=.047$), indicating that the ASD group showed a greater impairment, relative to controls, in the transpose condition than in the mirror condition. The interaction between the version and condition factors was also significant ($F(2,44) = 6.2$, $p=.004$). The requirement to transpose (i.e. to respond in a spatially incompatible manner) had a less detrimental effect on accuracy of responding in the verbal condition, where manual responses were not required.

If the poor performance of the ASD group in the imitative version of the task was due to an imitation-specific deficit, then the performance of the ASD group should have improved in the non-imitative versions of the pen-and-cups-task relative to any improvement shown by the control group. This would be manifested as a significant interaction between the version and group factors. This interaction was not significant ($F(2,44) < 1$). Of further theoretical interest is the three-way interaction between the version, group and condition factors, which could indicate improvement from the imitative to non-imitative version of the task in only one of the conditions. However, this interaction was also not significant ($F(2,44) < 1$).

The results of this analysis suggest that the ASD group were as impaired, relative to the control group, on both of the non-imitative versions of the task as on the original, imitative version. However, to test this conclusion further, analyses were carried out which separately compared each non-imitative version of the task with the imitative version.

ANOVA applied to the data from the geometric and imitative versions revealed significant main effects of group ($F(1,22) = 5.00$, $p=.036$) and condition ($F(1,22) = 30.00$, $p<.001$), reflecting the greater number of errors made by the ASD group in comparison to the control group and the increased difficulty of the transpose condition compared to the mirror condition. However, neither the interaction between the version and group factors ($F(1,22) < 1$), nor the three-way interaction between the version, group and condition factors ($F(1,22) < 1$) were significant.

Comparison of the verbal and imitative versions of the task using the same method demonstrated significant main effects of group ($F(1,22) = 6.2$, $p=.020$) and condition

($F(1,22) = 13.8$, $p=.001$), reflecting the greater number of errors made by the ASD group in comparison to the control group and the increased difficulty of the transpose condition compared to the mirror condition. In addition, the interaction between version and condition ($F(1,22) = 10.0$, $p=.005$) was significant, reflecting the greater effect of condition in the imitative version than in the verbal non-imitative version. Again however, neither the interaction between the version and group factors ($F(1,22) < 1$), nor the three-way interaction between the version, group and condition factors ($F(1,22) < 1$), was significant.

Participants in Experiment 3.2 completed two non-imitative versions of the pen-and-cups task and their performance was compared to that on the original, imitative version of the task. Since the initial purpose of this study was to investigate a previous finding, the order of tasks was not counterbalanced. However, this lack of counterbalancing is unlikely to have problematic implications for the conclusions of these experiments. One may expect performance to improve across tasks due to practice effects. Therefore, this feature of the design only served to make Experiment 3.2 a more conservative test of the hypothesis that there would be no improvement across tasks.

The results indicated that the ASD group was as impaired, relative to the control group, on the non-imitative versions of the task as they were on the imitative version of the task. Such a pattern of results suggests that this impairment is not imitation-specific. Although performance differences between the groups did not vary according to whether they completed imitative or non-imitative versions of the task, there was an overall tendency for the ASD group to show relatively poorer performance in the transpose conditions of the task.

3.3 General discussion

This chapter examined whether the impairments on tests of intentional imitation which have frequently been reported in ASD represent an imitation-specific impairment. To address this question, the performance of a group of high-functioning adults with ASD was compared with that of matched, typically-developing controls on an imitative, and two non-imitative, versions of the pen-and-cups task.

In common with previous reports of poor performance on imitation tasks, the ASD group made more errors than controls in Experiment 3.1, on the imitative version of the task. Experiment 3.2 tested whether this impairment was due to imitation-specific, or task-general, factors by asking the same participants to complete two non-imitative versions of the task. If the poor performance on the imitative version of the task was due to an imitation-specific impairment, one would expect improved performance when the task is changed so that it presents equally challenging general task demands, but is non-imitative. However, the ASD group was as impaired, relative to the control group, on each of the non-imitative versions of the pen-and-cups task. This pattern of results is inconsistent with claims of an imitation-specific impairment in ASD and suggests that impairments in general abilities, not specific to imitation, can account for the observed imitation impairments.

The present results are relevant both for theories of ASD as well as for theories of imitation. Some theories of ASD suggest that imitation represents the core deficit in ASD (e.g. Williams et al., 2001; 2004; Rogers & Pennington, 1991). In suggesting that observed imitation impairments may be accounted for by impairments in other general abilities, this chapter casts doubt on the idea that there is an imitation-specific impairment at the root of autism.

The present results are also of relevance to theories of imitation and specifically to the topics discussed in this thesis. An imitation-specific impairment in ASD would appear consistent with the idea that there is a special-purpose mechanism mediating imitation because this mechanism should be susceptible to selective impairment. Therefore, insofar as the results cast doubt on the existence of such an imitation-specific impairment, the present results suggest that the ASD literature may not provide any specific support for specialist claims. Therefore, the results from this chapter challenge evidence that can be used to support specialist theories of imitation.

The results from this chapter further challenge evidence used to support specialist claims in demonstrating the typical cup<hand<grip error pattern among individuals with ASD. If this error pattern relies on mentalistic goal attribution, one would not expect to see this error pattern in individuals with ASD who typically show mentalising impairments (e.g. Frith & Frith, 2003). However, if this pattern is due to general perceptual and attentional processes then one may expect similar patterns to be observed in individuals with ASD. This finding, therefore, supports the conclusions of Chapter 2 that the cup<hand<grip error pattern in the pen-and-cups task is due to the operation of general, perceptual and attentional processes, and not to the operation of an imitation-specific process which prioritises mentalistic goals.

The results from this study are consistent with some previous findings within the ASD imitation literature but are inconsistent with others. It is important to try to make sense of conflicting findings so that these experiments do not add confusion to a body of literature which already contains much disagreement.

The results of Experiment 3.1, which showed poor imitative performance among individuals with ASD, are consistent with the majority of previous findings. Like the present study, the majority of previous studies have employed complex intentional imitation tasks to assess imitative abilities in ASD. Given that the results from the present study suggest that poor performance on complex imitation tasks may be explained by non-specific impairments, poor performance observed in previous studies may also have been due to these non-specific factors. As highlighted in the first chapter, this idea has already been suggested by a number of authors who have found correlations between imitation performance and processes not specific to imitation, such as motor control and social reciprocity (Smith & Bryson, 1998; Green et al., 2002; McDuffie et al., 2007). However, previous studies were not able to determine whether there is an imitation impairment over and above these other more general processes. In Experiment 3.2, no differences were observed between the imitative and non-imitative tasks in the individuals with ASD. The present findings, therefore, suggest that, at least in the pen-and-cups task, the observed imitation impairment can be fully explained by processes not specific to imitation and that there is no additional imitation impairment associated with ASD.

The idea that any observed imitation impairment is a product of other, more general impairments may explain some of the mixed findings in the ASD literature. It is possible that in studies reporting equivalent performance on intentional imitation tasks for ASD and control groups (Aldridge, Stone, Sweeney, Bower, 2000; Carpenter, Pennington, & Rogers, 2001; Hamilton et al., 2007), general task demands were not sufficient to create group differences. Alternatively, the substantial heterogeneity within ASD could explain the mixed findings.

Experiment 3.1 did not replicate the particular pattern of errors reported by Avikainen et al. (2003), who found that the ASD group failed to benefit from imitating in a mirror fashion. In contrast, the ASD group in the present chapter benefited as much as the control group from mirror imitation. In fact, the ASD group showed a greater impairment in performance on the transpose versions of the pen-and-cups task. An impairment in transposition imitation is consistent with the inhibition problems reported in ASD (Russell, 1997). Many studies have demonstrated that spatially compatible responses are faster and more accurate than spatially incompatible responses (Simon, 1969). In the transpose condition, the tendency to make a spatially compatible response (which would result in mirror imitation) has to be inhibited. An inhibition impairment would result in increased mirror imitating, and therefore more errors in the transpose condition. However, this explanation is at odds with the findings of Avikainen et al. One possible reason for the conflicting results may be differences in the instructions used for the mirror condition. In the present experiment participants were explicitly told how to map stimuli onto responses (e.g. to use their right hand when the model used her left hand, and to use their left hand when the model used her right hand), while in the Avikainen et al. study participants were told only to "imitate as if looking in a mirror". The less explicit instructions used in the Avikainen et al. study may have caused uncertainty in the ASD group, and thereby masked any performance improvement which could have been observed when mirror imitating. This explanation is clearly speculative, and the effect of imitative frame of reference is a potential area for future research in ASD.

In summary, Experiment 3.1 demonstrated that this particular sample of high-functioning adults with ASD showed impaired performance on a test of intentional imitation. The results of Experiment 3.2 implied that the impaired performance shown

by this group on the test of imitation was not due to an imitation-specific impairment, because performance was equally impaired on two non-imitative versions of the task. Therefore, these experiments demonstrated that individuals with ASD may show impairments on tests of intentional imitation, not because of an imitation-specific impairment, but because of impairments in task-general mechanisms. The current results, therefore, challenge one line of evidence that has been used to support the idea that imitation is mediated by a special-purpose mechanism by suggesting that the core mechanisms of imitation are intact in ASD. This hypothesis will be further examined in the following chapter.

Chapter 4: Automatic imitation in individuals with ASD:

Intact imitation performance in ASD

Chapter 3 demonstrated that the poor performance on imitation tasks of individuals with ASD can be explained with reference to general processes, not specific to imitation. If this is correct, then there may not be an imitation-specific impairment in ASD. The purpose of this chapter was to provide a further test of whether or not individuals with ASD exhibit an imitation-specific impairment by using an automatic imitation task.

As highlighted throughout this thesis, successful imitation requires the translation of sensory information received from observing an action into the motor output required to perform a matching action. This translation represents the core mechanism of imitation and if there is an imitation-specific impairment in ASD, it is this mechanism that is disturbed. Alternatively, as suggested in Chapter 3, impairments in processes not specific to imitation create apparent imitation impairments. Under this view, there is no imitation-specific impairment in ASD.

The large body of literature demonstrating poor performance on a range of imitation tasks and the increasing number of studies showing mirror neuron dysfunction, in ASD, have been used to support the idea that individuals with ASD exhibit imitation-specific impairments (e.g. Williams et al., 2001; Dapretto et al., 2006). However, there are many inconsistent findings within this literature and the neurological literature, in particular, does not yet provide a clear message.

Furthermore, as highlighted in Chapters 1 and 3, the majority of studies investigating imitative abilities in ASD have used complex intentional imitation tasks. If poor performance on these tasks can be explained by impairments in other processes, not specific to imitation, then these studies do not tell us whether there is an imitation-specific impairment in ASD.

The previous chapter suggested that performance on these tasks can be explained by impairments in non specific processes, and therefore, complex intentional imitation tasks are not the best means for examining imitation skills in ASD. Automatic imitation tasks may be more informative than intentional imitation tasks in resolving whether or not there is an imitation-specific impairment in ASD. In tests of intentional imitation, the experimenter asks the participant to copy an action that has many temporal and spatial features, and does not specify exactly which features of the action are to be reproduced. Determining the appropriate action dimensions for imitation, and therefore, what constitutes successful performance, is accomplished through the interpretation of subtle cues relating to the social context and the experimenter's mental states. The ability to focus on the selected action dimensions, so that performance is not impaired by imitation of task-irrelevant action dimensions, relies on good executive function and attentional control. Interpretation of social cues, theory of mind, executive functions and attentional control have all been shown to be impaired in ASD (Bird et al., 2006; Frith & Frith, 2003; Russell, 1997). Therefore, poor performance in these intentional tasks may be due to impairments in these processes which are not specific to imitation.

In contrast, in tests of automatic imitation, participants are not asked, and do not intend, to imitate modelled movements. Instead, they are required merely to observe

actions, either passively or with a simple non-imitative movement task, while the experimenter measures muscular responses (e.g. Brass et al., 2001; Heyes et al., 2005). Consequently, automatic imitation tasks minimise the demands made on non-specific mechanisms.

The present study assessed imitation in high-functioning adults with ASD using an automatic imitation procedure. Only one study to date has tried to investigate automatic imitation in ASD. McIntosh, Reichmann-Decker, Winkielman & Wilbarger (2006) used electromyography (EMG) to measure muscular activity in the face while participants were presented with emotional facial expressions. Compared with controls, individuals with ASD showed less expression-compatible muscular activation. However, this study did not distinguish automatic imitation from emotional contagion. It is not clear whether, in the controls, observation of a smiling face promoted smiling directly, or by inducing positive affect. The results are also difficult to interpret because face stimuli were presented, and there is a growing body of evidence that gaze patterns to faces are abnormal in ASD (Klin, Jones, Schultz, Volkmar, & Cohen, 2002). Specifically, individuals with ASD spend less time looking at the eye-region of the face, which has been shown to be crucial in emotion recognition (Spezio, Adolphs, Hurley, & Piven, 2006).

To overcome these problems, affectively-neutral hand movements were used in the present study. Participants were required to perform a pre-specified hand movement (opening or closing) as soon as they saw a hand stimulus begin to move. They were, therefore, required to make the same movement (opening or closing) throughout each block. The movement of the hand stimulus was either the same as (compatible trials), or the opposite of, the pre-specified response (incompatible trials).

This task represents a more 'pure' test of imitation for a number of reasons. First, this paradigm investigates automatic imitation, thereby reducing the many task demands necessary for intentional imitation tasks, as highlighted above. Second, the required movements are very simple, and therefore, make few demands on motor control. Third, since participants are required to make one pre-specified movement per block, the instructions are simple and easy to comprehend. Therefore, the task does not require complex language comprehension skills. Furthermore, since there is only one simple task instruction and one movement to perform per block, the present task does not place many demands on working memory.

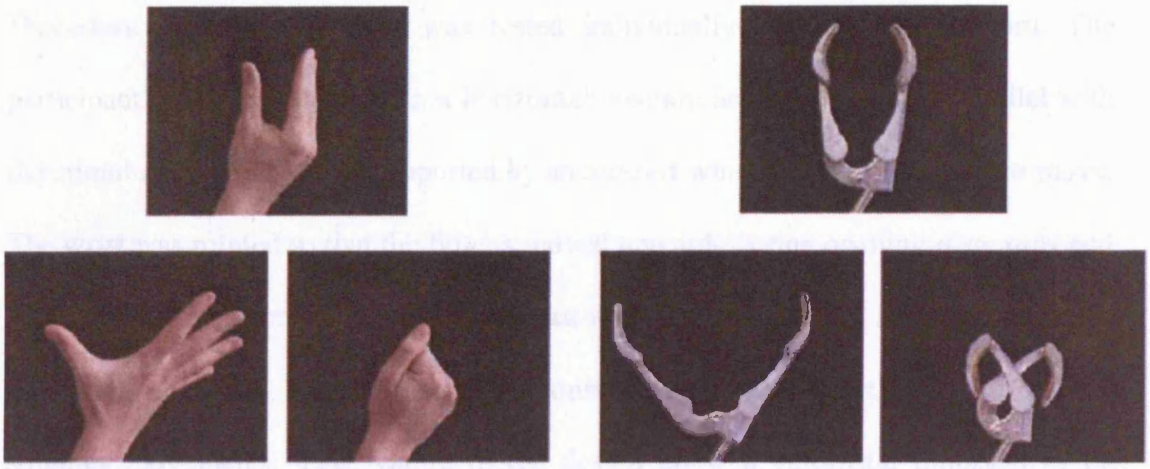
Previous studies using this paradigm have found two effects. First, a basic automatic imitation effect: responding is faster on compatible than on incompatible trials (Heyes et al., 2005). Second, an 'animacy effect': the automatic imitation effect is greater when the observed action is performed by a human effector than when it is performed by a human-like mechanical device, or 'robot' (Press et al., 2005; Kilner et al., 2003). It has been argued that the latter effect is a direct consequence of increased mirror system activity in response to observation of human, compared to robotic, action (Tai et al., 2004). Thus, Experiment 4.1 sought to investigate automatic imitation and the animacy effect in a group of high-functioning adults with ASD and typically-developing matched controls. If an imitation-specific impairment exists in ASD, individuals should show a smaller automatic imitation effect and a smaller animacy effect than controls. Conversely, if there is no imitation-specific impairment, individuals with ASD should show automatic imitation and animacy effects comparable to those of controls.

Experiment 4.1

4.1.1. Method

Participants. Thirty-two individuals participated in the study: 16 with ASD (15 male; 1 female) and 16 typically developing controls (15 male; 1 female). Participants were recruited from the UCL, Institute of Cognitive Neuroscience database. Groups were matched on gender, age (ASD M: 34.9 years SEM: 3.2, control M: 33.2 years, SEM: 3.4), and IQ (ASD FSIQ M: 110, SEM: 3, VIQ M: 110, SEM: 3, PIQ M: 106, SEM: 4 Control FSIQ M 112, SEM: 3, VIQ M: 111, SEM: 3, PIQ M: 108, SEM: 2). IQ was measured using the Wechsler Adult Intelligence Scale-3rd UK Edition (Wechsler, 1999). All participants in the ASD group had previously received a diagnosis from an independent clinician according to standard criteria. The Autism Diagnostic Observational Schedule-G (Lord et al., 2000) was used in order to characterize the participants. On this measure, nine participants met criteria for autism, while seven participants met criteria for autism spectrum disorder. All participants were right-handed, had normal or corrected-to-normal vision and were naive with respect to the purpose of the experiment.

Stimuli. All stimuli were presented on an LCD laptop computer screen (60Hz, 400mm, 96 DPI) in colour on a black background (see Figure 1). Each imperative stimulus was a photograph of a human or a robotic hand in an opened or a closed posture. It was preceded by a warning stimulus representing a neutral posture of the same hand type (human or robotic). The transition from the warning to the imperative stimulus induced apparent motion so that the hand appeared to start in the neutral position and then to open or to close.



(a) (b)

Figure 10: Experiment 4.1. Images depicting the warning stimuli (top) and opening and closing stimuli for a) the human and b) the robot stimulus types.

Data recording and analysis. For both open and close responses, response onset was measured by recording the electromyogram (EMG) from the first dorsal interosseus (FDI) muscle of the right hand. Signals were amplified, high-pass filtered at 20Hz, mains-hum filtered at 50Hz and digitised at 2.5kHz. They were rectified and smoothed using a dual-pass Butterworth filter, with a cut-off frequency of 50Hz. Signals were not low-pass filtered. To define a baseline, EMG activity was registered for 100ms when the participant was not moving at the beginning of each trial. A window of 20ms was then shifted progressively over the raw data in 1ms steps. Response onset was defined by the beginning of the first 20ms window after the imperative stimulus in which the standard deviation for that window, and for the following 20ms epoch, was greater than 2.75 times the standard deviation of the baseline. This criterion was chosen during initial calibration of the equipment as the most effective in discriminating false positives from misses. Whether the criterion correctly defined movement onset in the present experiment was verified by sight for every trial performed by each participant. Stimulus onset marked the beginning, and EMG onset marked the end, of the response time (RT) interval. Errors were recorded manually.

Procedure. Each participant was tested individually in a dimly lit room. The participant's right forearm lay in a horizontal position across their body, parallel with the stimulus monitor. It was supported by an armrest which allowed the hand to move. The wrist was rotated so that the fingers moved upwards during opening responses and downwards when closing. Stimulus postures were presented in the lateral plane (left–right), and therefore, the direction of response movements was orthogonal to that of stimulus movements. This feature of the design allowed automatic imitation to be isolated from left-right spatial compatibility. After each response, participants returned their hand to the neutral starting position. In each block participants were instructed to make a pre-specified response (open or close) as soon as possible after the movement stimulus appeared. Thus, although voluntary actions were performed, any effect of imitation on those actions was automatic in the sense that participants were neither instructed nor intended to imitate. Participants were instructed to refrain from moving their hands in catch trials, when the imperative stimulus was not presented.

All trials began with presentation of the warning stimulus. In stimulus trials, this was replaced 800–1500ms later by the movement stimulus, which was of 480ms duration. The stimulus onset asynchrony (SOA) varied randomly between 800 and 1500ms. After the movement stimulus, a blank screen was presented (3000ms) before the next trial. In catch trials, the warning stimulus remained on the screen for 1980ms before the blank screen was presented for 3000ms. Each block presented, in random order, 15 trials in which the hand stimulus opened, 15 trials in which the hand stimulus closed, and 6 catch trials. Thus, in each block, there were 15 trials in which the response and stimulus movements matched ('compatible trials') and 15 in which the stimulus and response movements did not match ('incompatible trials').

Human and robotic stimuli were presented in separate blocks. Participants, therefore, completed four blocks in total, two in which closing was the required response and two in which opening was the required response. Response order (open or close first), and stimulus type (human or robotic) were balanced across participants. Before each block, participants completed five practice trials with the response, and the stimuli, to be used in that block.

4.1.2. Results

Incorrect responses (e.g. hand opening when closing was required, 0.05%) were excluded from the analysis, as were all RTs smaller than 100 ms and greater than 1000 ms (0.05%). On each trial, the stimulus movement was either the same as (compatible) or different from (incompatible) the pre-specified response. The RT data are given in Table 2, and the compatibility effects (the difference in RT between compatible and incompatible trials) are shown in Figure 11.

	Human Action		Robotic Action	
Group	Compatible Trials	Incompatible Trials	Compatible Trials	Incompatible Trials
ASD	347 (18)	403 (22)	345 (18)	365 (17)
Control	303 (16)	342 (17)	313 (19)	337 (17)

Table 2: Experiment 4.1. Mean (and standard error of the mean) RT (ms) for both groups on compatible and incompatible trials in response to human and robotic action

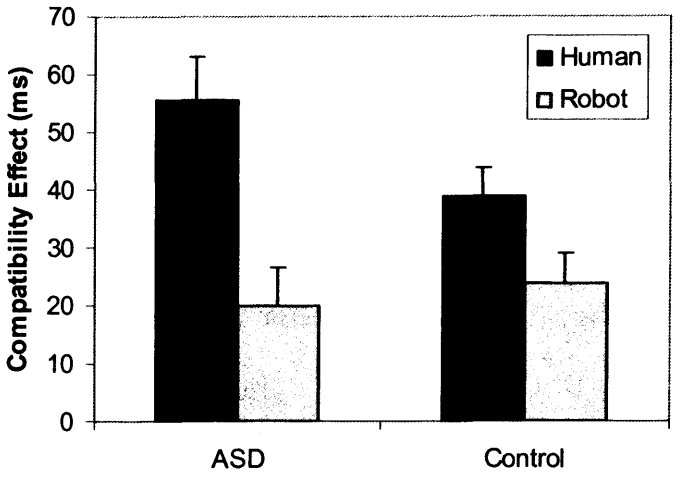


Figure 11: Experiment 4.1. The mean compatibility effect (RT on incompatible trials - RT on compatible trials) for human (black bars) and robot stimuli (grey bars) in the ASD and control groups. Vertical bars indicate standard error or the mean.

The RT data were analysed using ANOVA with within-subject factors of trial type (compatible and incompatible), stimulus type (human and robotic) and a between-subjects factor of group (ASD and control). This analysis revealed a significant main effect of trial type ($F(1,30) = 79.0$, $p<0.001$) due to faster responses on compatible trials (mean: 327.1, SEM: 11.9) than incompatible trials (mean: 361.6, SEM: 12.6). The interaction between trial type and stimulus type was also significant ($F(1,30) = 29.6$, $p<0.001$): the compatibility effect was greater when responding to a human (mean: 47.2, SEM: 1.9) compared with a robot stimulus (mean: 21.9, SEM: 1.1). The three-way interaction between group, trial type, and stimulus type was also significant ($F(1,30) = 4.6$, $p = 0.04$), indicating that the difference between the human and robotic compatibility effect was *larger* in the ASD group (mean: 35.3, SEM: 3.9) than in the control group (mean: 15.3, SEM: 3.9). No other main effects or interactions were significant (all p values >= .10).

Simple effects analysis was used to examine the three-way interaction between group, trial type and stimulus type. This revealed that the compatibility effect (control

$F(1,15) = 57.9$, $p<0.001$; ASD $F(1,15) = 32.9$, $p<0.001$), and the animacy bias (control $F(1,15) = 5.6$, $p = 0.03$; ASD $F(1,15) = 27.8$, $p<0.001$) were both significant in each group. The ASD group exhibited a trend towards a greater compatibility effect when responding to observed human actions ($F(1,30) = 3.0$, $p = 0.09$) than the control group. The groups did not differ in the magnitude of their compatibility effect when responding to observed robotic actions.

4.2 Discussion

Experiment 4.1 examined automatic imitation of simple hand actions in ASD. Like typically-developing controls, the ASD group showed a significant automatic imitation effect and a significant animacy bias effect. Furthermore, the results from this study demonstrated a surprising finding, whereby individuals with ASD showed an increased animacy bias compared to controls.

The first of these findings, and the principal finding of this experiment, is that individuals with ASD showed intact automatic imitation. This was demonstrated both by a compatibility effect and an animacy bias comparable to the effects observed in controls. The results from this chapter are, therefore, consistent with the hypothesis that individuals with ASD do not exhibit an imitation-specific impairment.

In this respect, the current results are consistent with some other studies that have found intact imitative performance among individuals with ASD (e.g. Carpenter et al., 2001; Hamilton et al., 2007). However, they are not consistent with the majority of research in this area (Williams et al., 2004). However, because the majority of previous tasks used tests of intentional imitation, the fact that they found impaired performance does not necessarily mean that individuals with ASD exhibit an imitation-specific

impairment. As suggested in Chapter 3, performance in tests of intentional imitation is vulnerable to the effects of non-specific factors such as theory of mind and executive function impairments. Therefore, poor performance on these complex intentional tasks may have been due to impairments in these abilities rather than to impairments in imitation-specifically. By reducing task demands, such as executive function, theory of mind and motor control, the present study allowed imitative abilities of individuals with ASD to be examined using a more pure test of imitation. Thus, this task permitted a demonstration of intact imitative performance in this group.

However, it is necessary to consider the possibility that the equivalent performance shown by the ASD and control groups in Experiment 4.1 was not an artifactual 'null result' due to insufficient statistical power. Several factors suggest that this was not the case. First, the ASD group were significantly faster to make a pre-specified hand movement when it was imitative, than when it was non-imitative, and thus demonstrated an automatic imitation effect. Second, the ASD group showed a greater degree of automatic imitation in response to human than to robotic actions, and thus showed the typical animacy bias effect. Third, group comparisons revealed that the amount of automatic imitation shown by the ASD group in response to human actions was numerically greater than that of the control group and this difference approached statistical significance. Fourth, the ASD group showed a significantly *greater* animacy bias than the control group, i.e. the extent to which human actions were imitated more than robotic actions was significantly greater in the ASD group than the control group.

The second interesting finding generated by this study was that individuals with ASD displayed an increased animacy bias compared to controls. On this basis, it could be argued that individuals with ASD showed a *greater* tendency to imitate than controls.

Inspection of the mean RT data suggests that this increased animacy bias was largely due to enhanced automatic imitation of human actions. This finding should be interpreted with caution as the simple interaction between the group and trial type factors with human stimuli only approached statistical significance. However, this pattern of data is interpretable.

Enhanced automatic imitation of human stimuli may arise from an inability to inhibit an imitative response. This idea is consistent with recent evidence suggesting a link between theory of mind and the ability to inhibit imitation. It has been shown that imitation inhibition and theory of mind are mediated by overlapping areas of the prefrontal cortex (Brass, Derrfuss & von Cramon, 2005), and a positive correlation between the ability to inhibit imitation and performance on theory of mind tasks has been found in patients with both frontal and posterior brain lesions (Brass, Derrfuss, Matthes-von Cramon, & von Cramon, 2003). The authors of these studies argue that representing both the self and other, which relies on the theory of mind system, is a crucial component of imitation inhibition. Theory of mind deficits are well-documented in ASD (e.g. Frith & Frith, 2003), and therefore it is plausible that the ASD group showed a greater compatibility effect due to problems inhibiting imitation on incompatible trials. Such a suggestion is also consistent with two clinical features of ASD which suggest imitation inhibition problems: echolalia and echopraxia.

The imitation inhibition hypothesis was tested by separately analysing incompatible trials (which require imitation inhibition) and compatible trials (which do not). In accordance with the prediction of the imitation inhibition hypothesis, the ASD group showed an increased animacy bias only on incompatible trials (group x animacy interaction: incompatible trials: $F(1,30) = 5.5$, $p = .026$; compatible trials: $F(1,30) < 1$),

and this was due to significantly slower responses on incompatible trials with human stimuli ($F(1,30) = 4.7$, $p=0.037$). This finding is therefore consistent with the idea that individuals with ASD have imitation inhibition deficits.

It is important to note that an imitation inhibition deficit in ASD would not constitute a specific imitation impairment because imitation inhibition is thought to rely on theory of mind skills. It is, therefore, likely that observed inhibition impairments are caused by impaired theory of mind abilities in individuals with ASD. Therefore, the imitation inhibition account of the enhanced animacy effect in ASD is consistent with the principal message of this chapter, that is, that there is no imitation-specific impairment in ASD.

In summary: the specificity of reported imitation impairments in ASD was investigated using an automatic imitation task. Rather than showing impairments, participants with ASD showed a typical automatic imitation effect and a typical animacy bias. This suggests that, in accordance with Chapter 3, previous findings of poor performance on tests of imitation may have been due to impairments of non-specific mechanisms that are recruited by both imitative and non-imitative tasks. The present findings imply that the core mechanisms of imitation, those that translate observed into executed actions, are intact in individuals with ASD.

Evidence of a specific imitation impairment in ASD has been used to support claims that imitation is mediated by a special-purpose mechanism. The findings from this chapter and the previous chapter, therefore, challenge these claims by suggesting that there is no specific imitation impairment in ASD. Consequently, the ASD literature may not be able to provide support for specialist claims.

Chapter 5: Automatic imitation in typically developing individuals: Effector-specificity in imitation: Support for generalist theories.

Intentional imitation is typically effector-specific. In everyday life and in the laboratory, when a person imitates an action, they reproduce the features of the modelled movement using the same part of the body. Hand movements are imitated with the hands, foot movements with the feet, and mouth movements with the mouth. This chapter examines effector-specificity in imitation to ascertain whether the effector-specificity of intentional imitation reflects the structure of the core mechanisms of imitation and, if so, what it can tell us about the specialist or generalist nature of those mechanisms.

A number of studies demonstrate that, when required to imitate, children and adults reproduce modelled movements using the modelled effector system (Franz, Ford & Werner, 2007; Head 1920; Wapner & Cirillo, 1968; Wohlschläger et al., 2003). This is the case even when instructions are non-specific; that is, when it is not specified exactly which features of an action should be imitated. For example, when an adult model faces a child, says 'Do this' or 'Do as I do', and raises a hand above his head, the child raises one of her own hands (Wapner & Cirillo, 1968); she does not raise a foot, or an eyebrow. Actions may be carried out using the spatially compatible or anatomically compatible side of the body and this laterality of participants' responses may vary according to age and task demands. For example, younger children, and adults under time pressure, tend to imitate right hand movements with the (spatially compatible) left hand and vice versa (Wapner & Cirillo, 1968; Wohlschläger et al., 2003). While laterality effects of this kind show that intentional imitation performance is flexible with respect to the side of the body used to reproduce the model's

movement, and that it is susceptible to spatial compatibility effects (Bird et al., 2007, Heyes & Ray, 2000), they do not represent a departure from effector-specificity, i.e. imitation of movements using the same effector *system*.

The effector-specificity of intentional imitation may reflect the structure of core mechanisms of imitation, or it may be largely conventional. As highlighted in previous chapters, the core mechanisms of imitation are those that solve the correspondence problem (Brass & Heyes 2005), translating visual input from observed body movements into matching motor output, and thus explaining *how* we imitate. It is possible that these mechanisms are effector-specific; for example, they may be incapable of translating observed movements of one effector system into motor output in another effector system. If so, then effector-specificity at the mechanism level could be responsible for the effector-specificity observed in intentional imitation performance. Alternatively, it may be that the core mechanisms of imitation are fully or partially effector-independent, and that intentional imitation behaviour is influenced by cultural knowledge. This hypothesis suggests that, within anatomical constraints, a participant observing a hand movement is enabled by core imitation mechanisms to reproduce the movement either with their hand or with an alternative effector system. However, when the participant is instructed to imitate, she chooses to use the same effector as the model because she understands, that effective imitation requires both movement and effector matching.

Studies of imitation in infancy suggest that the effector-specificity of intentional imitation is not purely conventional. Effector-specific imitative responses have been observed in young infants. For example, observation of tongue protrusion increases the probability of tongue protrusion, but not of lip protrusion (Meltzoff & Moore, 1977;

1983; 1989; 1997). Given the age of the infants in these studies (some as young as 72 hours), it is highly unlikely that their behaviour was guided by inferences about what was required in the test situation or what is required for effective imitation. However, these findings do not provide conclusive evidence that the mechanisms of imitation are effector-specific, because, as discussed in section 1.2.2, the tendency of infants to respond to tongue protrusion with tongue protrusion may be mediated by arousal processes, rather than by the mechanisms that mediate imitation later in development (Anisfeld, 1991; 1996; Jones, 1996; 2006; Ullstadius, 1998).

Like infancy research, some recent studies of automatic imitation in adults provide suggestive evidence that it is the mechanisms of imitation which are effector-specific. Performance in automatic imitation tasks is unlikely to be influenced by inferences about the experimenter's expectations because these tasks examine imitation under conditions in which participants are not told to imitate, may not be aware that they are imitating, and in which imitation can interfere with the efficient execution of task instructions (e.g. Brass et al., 2000; Craighero et al., 1998; Heyes et al., 2005; Lakin & Chartrand, 2003; Stanley, Gowen, Miall, in press; Stürmer et al., 2000). In a study of this kind, Chartrand & Barge (1999) found that, when a model and an observer were in conversation, observation of face rubbing elicited more face rubbing than foot shaking, and vice versa for observation of foot shaking. Similarly, in a choice RT task, Bach & Tipper (2007) asked participants to identify a model as either 'George' or 'John' by pressing a button with their foot or with their hand, and found that observation of the model performing foot actions (kicking a ball) facilitated foot responses, whereas observation of the model performing hand actions (typing on a keyboard) facilitated hand responding. These studies, and others like them (Berger & Hadley, 1975; Bertenthal et al., 2007; Brass et al., 2000; Gillmeister et al., under review), suggest that

observation of an effector in motion selectively activates responses made with the same effector. However, they do not tell us whether this 'effector priming' effect is specific to movements that match those observed. Therefore, although effector priming is of interest in its own right, its occurrence does not necessarily imply that the mechanisms mediating imitation are effector-specific. To find out whether this is the case, it would be necessary to dissociate movement type (e.g. rubbing vs. shaking, kicking vs. typing) from effector type (e.g. feet vs. hands), and to show that observation of a particular movement type is more likely to elicit an imitative response when the response is performed with the modelled effector than when it is performed with an alternative effector. This logic was applied in Experiments 5.1 and 5.2.

The effector-specificity of imitation was investigated using a SRC automatic imitation procedure (e.g. Bertenthal et al., 2006; Brass et al., 2000; Heyes et al., 2005; Kilner et al., 2003; Press et al., 2005; Stürmer et al., 2000). In each trial of the choice RT task, participants were required to make one of four responses: to open their hand, to close their hand, to open their mouth, or to close their mouth. The correct response for each trial was indicated by a pair of letters presented on a computer screen. The letters were accompanied by one of four, task-irrelevant action stimuli: a photographic image of an open hand, a closed hand, an open mouth, or a closed mouth. Thus, the irrelevant action stimulus and the correct response were either effector compatible and movement compatible (e.g. open hand stimulus and open hand response), effector compatible and movement incompatible (e.g. close hand stimulus and open hand response), effector incompatible and movement compatible (e.g. open mouth stimulus and open hand response) or effector incompatible and movement incompatible (e.g. close mouth stimulus and open hand response).

Previous SRC studies, in which responses were effector compatible, have shown a movement compatibility effect for hand opening and closing responses; e.g. hand opening is initiated faster in response to a hand opening than to a hand closing stimulus (Heyes et al., 2005; Stürmer et al., 2000). They have also shown that this effect is not due to left-right or orthogonal spatial relations between the stimuli and responses (Press et al., under review). In line with these findings, in the present chapter, a movement compatibility effect was expected when the stimulus and the response effector were compatible. The primary focus of interest was the relative magnitude of any movement compatibility effect in the effector compatible and the effector incompatible conditions. If imitation mechanisms are effector-independent, rather than effector-specific, then the movement compatibility effect should be equally strong in the effector compatible and the effector incompatible conditions. This would be a surprising result, given previous evidence of effector priming, but it would be interpretable, suggesting that the effector-specificity of intentional imitation is conventional or, more broadly, a product of high-level cognitive processes influencing the output from core mechanisms of imitation.

Three of the theories of imitation addressed in this thesis, the ASL model, (Heyes & Ray, 2000; Heyes, 2001), IM (Prinz 1997; 2002) and the AIM theory (Meltzoff & Moore, 1997) suggest that imitation mechanisms are effector-specific. Thus, these theories would predict an interaction between movement compatibility and effector compatibility in the present study. However, whereas ASL and IM predict partial effector-specificity, AIM predicts total effector-specificity. Therefore, the generalist theories predict a smaller but detectable movement compatibility effect in the effector incompatible condition, and the AIM model predicts the absence of any movement compatibility effect when responses are made with an incompatible effector.

These predictions follow from the assumptions of each theory. The ASL model (Heyes & Ray, 2000; Heyes, 2001) assumes that imitation is mediated by a repertoire of 'vertical associations', each linking a sensory representation of an action with a motor representation of the same action. Sensory and motor representations can each include information about the movement and the effector properties of the represented action, and the links between them are acquired in the course of development through associative learning. Their formation depends on correlated experience of observing and executing the same action. Responses that are based on associative learning are known to show stimulus generalization; stimuli that were not present during training elicit the response to the extent that they are physically similar to the training stimuli (Pearce, 1987; 1994). Therefore, although it is unlikely that participants will have experienced a reliable correlation between observation of hand opening and execution of mouth opening, for example, the ASL model predicts some facilitation of mouth opening by observation of hand opening because, when they are observed, hand opening resembles mouth opening. For example, both movements involve the separation of two salient objects, the lips in the case of mouth opening, and the fingers and thumb in the case of hand opening. Stimulus generalization, therefore, should lead to partial effector-specificity of imitation.

Partial effector-specificity of imitation would also be predicted by IM, which suggests that actions are represented in terms of their sensory consequences, and that action observation primes performance of an action to the extent that the observed and executed actions have similar sensory consequences. Therefore, the observation of a hand opening will activate any action representation with which it shares some degree of ideomotor similarity. The action representation which exhibits the greatest degree of similarity will be activated most strongly, and this is likely to be the 'hand opening'

action representation. However, since mouth opening and hand opening share some physical characteristics, and therefore, some ideomotor similarity, observation of a hand opening action may activate a 'mouth opening' action representation, and therefore, prime a mouth opening response, but to a lesser extent.

In contrast with the partial effector-specificity proposed by ASL and IM, the AIM theory assumes that imitation is a two-stage process: "an imitative act is not one indissociable unit. It can be differentiated into organ [effector] identification and movement components" (Meltzoff & Moore, 1997, p184). The first, 'organ identification', stage identifies the effector system used by the model, leads to generalized activation of the observer's corresponding effector system (effector priming), and to inhibition or 'quietening' of the observer's other effector systems. The second stage, the 'movement component', identifies the movement properties of the modelled action, codes these as 'organ relations' (e.g. 'tongue-to-lips'), and, via this coding, activates or facilitates execution of the same movement by the observer. This model implies that the second stage mechanisms, those that mediate movement imitation, are effector-specific; that they apply effector-specific codes (e.g. tongue-to-lips), and enable matching movements only of the effector system selected at the organ identification stage. If, as AIM proposes, the movement matching process is based on effector-specific codes, then, in the present study, one would not expect an effect of movement compatibility when responses are made with the incompatible effector.

To summarize, an automatic imitation SRC procedure was used to investigate the effector-specificity of the mechanisms that mediate imitation. In this procedure, participants made opening and closing movements of the hand and of the mouth in the presence of task-irrelevant action images that were effector and movement compatible,

effector compatible and movement incompatible, effector incompatible and movement compatible, or effector and movement incompatible with the required response. A movement compatibility effect in the effector compatible condition (e.g. faster hand opening responses in the presence of open than of close hand stimuli) was expected on the basis of previous studies. An equally strong movement compatibility effect in the effector incompatible condition (e.g. faster hand opening responses in the presence of open than of close mouth stimuli), would suggest that imitation mechanisms are effector-independent. A weaker, but significant, movement compatibility effect in the effector incompatible than in the effector compatible condition would indicate that movement imitation is partially effector-specific, and would be consistent with the views of ASL and IM regarding the mechanisms that mediate imitation. The absence of a movement compatibility effect in the effector incompatible condition would indicate that movement imitation is wholly effector-specific, and would be consistent with the account of imitation mechanisms provided by AIM.

Experiment 5.1

Participants were instructed to make one of four responses to letters on a computer screen. They were told to open their mouth if the letters were 'om', to close their mouth in response to 'cm', to open their hand in response to 'oh' and to close their hand in response to 'ch'. Participants were also told that the letters would appear with irrelevant images of hand and mouth movements, which they should ignore. The irrelevant stimuli depicted a hand either opening or closing or a mouth opening or closing. Therefore, for any given trial, the response effector was either compatible or incompatible with the irrelevant stimulus effector and the response movement was either compatible or incompatible with the irrelevant stimulus movement. There were,

therefore, two types of compatibility (effector and movement), and each had two levels (compatible and incompatible).

5.1.1 Method

Participants. Thirteen consenting, healthy participants with an average age of 25.7 years, 7 male, were recruited from the UCL Department of Psychology database and paid a small honorarium for their participation. All were right-handed, had normal or correct-to-normal vision, and were proficient in the English language. They were naïve with respect to the purpose of the experiment.

Stimuli and apparatus. All stimuli were presented on an LCD laptop computer screen (60Hz, 400mm, 96 DPI) in colour on a black background. Viewing was unrestrained at a distance of approximately 600mm. Warning stimuli consisted of photographic images of two effectors side-by-side, a mouth and a right hand, each in a neutral posture (Figure 12). In half of the trials the hand was on the left of the screen with the mouth on the right, and in the other half, this configuration was reversed.

Each imperative stimulus consisted of the hand and mouth images in the same left-right position as in the preceding warning stimulus, but one effector was displayed in an open or close posture, whereas the other remained in the neutral posture. Additionally, between the effectors, in the centre of the screen, two letters were displayed, one above the other.

The letters were in Arial font size 28, lower case, and printed in white on a black background. The two letters combined occupied 1.0° (width) x 2.4° (height) of viewing angle. The hand and mouth stimuli were matched in terms of the overall area

of the stimulus in the neutral position, the open position and the close position. In the neutral position, the hand occupied 3.3° (width) x 5.7° (height) of viewing angle and the mouth occupied 3.3° (width) x 5.2° (height) of viewing angle. The distance between the middle finger and thumb when the hand was in the neutral position occupied 1.4° of viewing angle and the distance between the top and bottom lip when the mouth was in the neutral position occupied 1.6° of viewing angle. The distance between the middle finger and thumb when the hand was in the open position occupied 5.2° of viewing angle and the distance between the top and bottom lip when the mouth was in the open position occupied 5.0° of viewing angle. In the close position, the distance between the lips and between the fingers occupied 0° of viewing angle.

There were four letter pairs (ho, hc, mo, mc), each consisting of a letter indicating the correct response effector (h for hand or m for mouth) and a letter indicating the correct response movement (o for open or c for close). In half of the imperative stimuli the letter representing the effector was placed above the letter representing the movement, and in the other half this configuration was reversed.

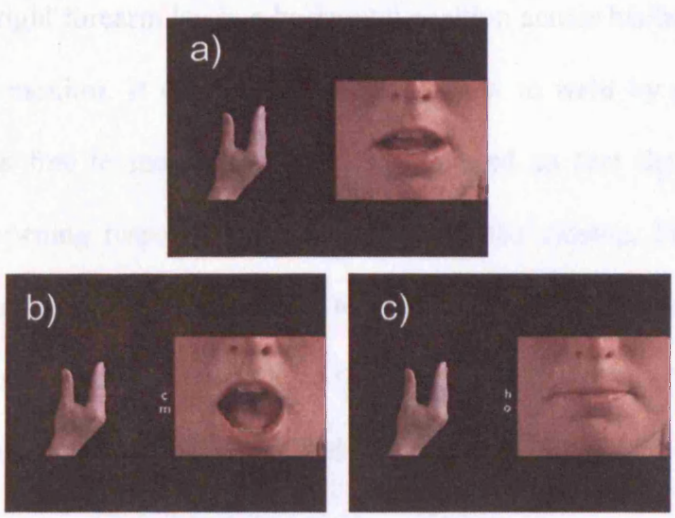


Figure 12: Experiment 5.1. Images depicting a) the neutral warning stimulus, b) and c) two examples of imperative stimuli. In Figure 12b the irrelevant stimulus (open mouth) is effector compatible and movement incompatible with the required response (close mouth). In Figure 12c the irrelevant stimulus (close mouth) is effector incompatible and movement incompatible with the required response (open hand).

Data recording and analysis. For both open and close responses, response onset was measured by recording the electromyogram (EMG) from the first dorsal interosseus (FDI) muscle in the hand and the orbicularis oris (OO) in the mouth using disposable Ag/AgCl surface electrodes. Recording electrodes were placed on the OO on the right hand corner of the mouth and on the FDI on the right hand. The signal pre-processing and EMG recoding procedures were identical to those described in Chapter 4.

Procedure. Each participant was tested individually in a dimly lit room. Participants were told that they would see some pictures of hands and mouths on either side of the screen, but that they should ignore the movements of these body parts and respond to the letters in the centre of the screen. It was explained that they should open their mouth in response to the letters 'om', close their mouth in response to 'cm', open their hand in response to 'oh' and close their hand in response to 'ch'. Participants were told to make their response as soon as the letter appeared on the screen but to keep as still as possible at all other times.

The participant's right forearm lay in a horizontal position across his/her body, parallel with the stimulus monitor. It was supported from elbow to wrist by an armrest such that the hand was free to move. The wrist was rotated so that the fingers moved upwards during opening responses and downwards when closing. Participants were shown the correct neutral positions for the hand and the mouth. In the neutral mouth position, participants were required to have their lips slightly parted. They were asked to return to the neutral position after they had made each response.

All trials began with presentation of the warning stimulus which was replaced 800-2000ms later by an imperative stimulus of 480ms duration. The SOA varied randomly

between 1200 and 2400ms in 400ms steps. After the imperative stimulus the screen went black for 3000ms before the warning stimulus for the next trial appeared.

Each block contained 128 trials in total, 32 trials of each of the four principal types (effector and movement compatible; effector compatible and movement incompatible; effector incompatible and movement compatible; effector and movement incompatible) in random order. In half of the trials of each type, the hand stimulus was on the left of the mouth stimulus, and in the other half it was on the right. Each participant completed two blocks of trials, one in which the effector indicator (h or m) was above the movement indicator (o or c), and the other in which it was below the movement indicator. Half of the participants completed the blocks in the order described, and half in the alternative order. Before testing commenced in each block, participants completed 10 practice trials consisting of a random selection of trial types from within that block.

5.1.2. Results and discussion

Practice trials, incorrect responses (3.9%) and response omissions (3.8%) were excluded from the analysis, as were all RTs smaller than 100ms and greater than 1500ms (0.05%). One participant, for whom more than 10% of the data were missing, was excluded from the analysis. The RT data from the remaining 12 participants are shown in Figures 13 and 14.

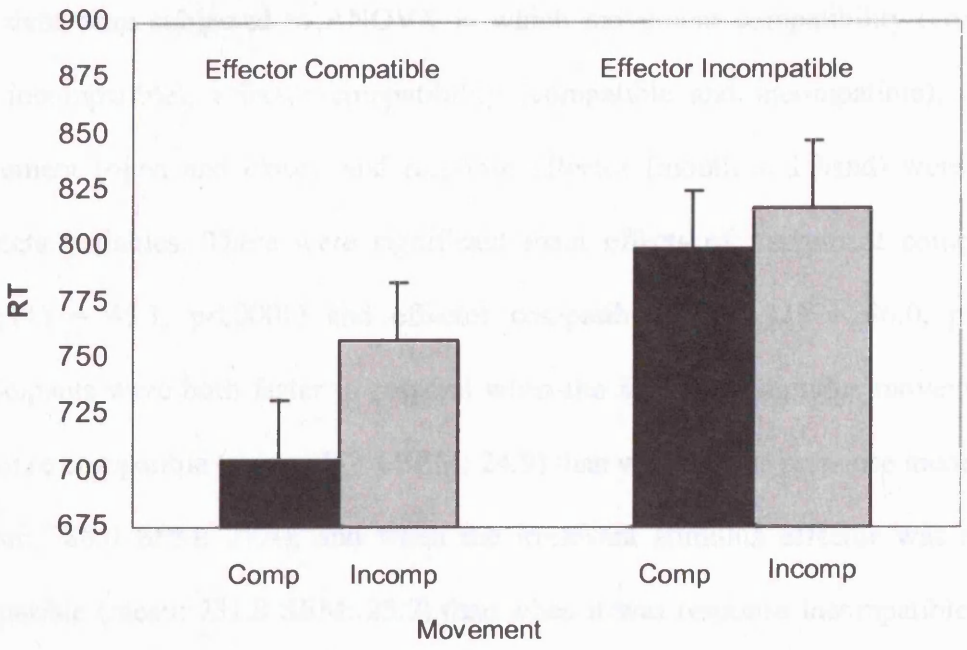


Figure 13: Experiment 5.1. Mean RT on movement compatible (black bars) and movement incompatible (grey bars) trials when effector was compatible (left side) and when it was incompatible (right side). Vertical bars indicate the standard error of the mean.

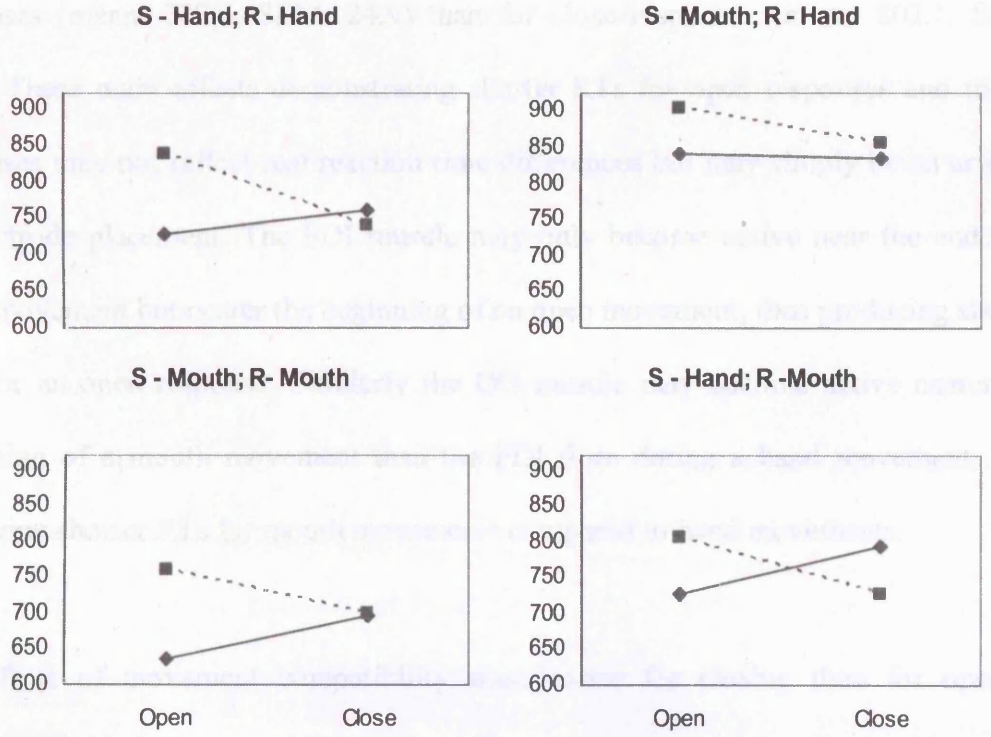


Figure 14: Experiment 5.1. Mean RT for open (diamonds and solid lines) and close (squares and dashed lines) movement responses for each trial type defined by the stimulus effector (S) and response effector (R) mapping.

The data were subjected to ANOVA in which movement compatibility (compatible and incompatible), effector compatibility (compatible and incompatible), response movement (open and close), and response effector (mouth and hand) were within-subjects variables. There were significant main effects of movement compatibility ($F(1,11) = 45.1$, $p<.0001$) and effector compatibility ($F(1,11) = 86.0$, $p<.0001$). Participants were both faster to respond when the irrelevant stimulus movement was response compatible (mean: 752.4 SEM: 24.9) than when it was response incompatible (mean: 788.0 SEM: 27.4), and when the irrelevant stimulus effector was response compatible (mean: 731.8 SEM: 25.7) than when it was response incompatible (Mean: 808.6 SEM: 27.0). There were also significant main effects of response effector ($F(1,11) = 32.8$, $p<.0001$), and of response movement ($F(1,11) = 21.7$, $p<.0001$). Shorter RTs were recorded for mouth responses (mean: 728.1, SEM: 26.6) than for hand responses (mean: 812.3, SEM: 27.6). Shorter RTs were also recorded for open responses (mean: 738.3, SEM: 24.9) than for close responses (mean: 802.1, SEM: 28.8). These main effects demonstrating shorter RTs for open responses and mouth responses may not reflect real reaction time differences but may simply be an artefact of electrode placement. The FDI muscle may only become active near the end of a close movement but nearer the beginning of an open movement, thus producing shorter RTs for an open response. Similarly the OO muscle may become active nearer the beginning of a mouth movement than the FDI does during a hand movement, thus producing shorter RTs for mouth movements compared to hand movements.

The effect of movement compatibility was greater for closing than for opening responses (movement compatibility x response movement, $F(1,11) = 5.6$, $p=.04$), but simple effects analysis confirmed that movement compatible responses were faster than movement incompatible responses both when the response was opening ($F(1,11)$

= 11.2, p<.006, compatible: mean: 727.7, SEM 25.4; incompatible: mean: 748.9, SEM: 24.9) and when it was closing (F(1,11) = 27.9, p<.0001, compatible: mean: 777.1, SEM; 26.4 incompatible: mean: 827.1, SEM: 31.8). Similarly, the effect of effector compatibility was greater when responses were made with the hand than when they were made with the mouth (effector compatibility x response effector, F(1,11) = 6.8, p=.03), but effector compatible responses were faster both for mouth responses (F(1,11) = 42.4, p<.0001, compatible: mean 697.6:, SEM: 25.8; incompatible: mean: 758.6, SEM: 28.1), and for hand responses (F(1,11) = 69.5, p<.0001, compatible: mean: 765.9, SEM: 27.9; incompatible: mean: 858.6, SEM: 28.3).

Of principal interest, given the purpose of the experiment, there was a significant movement compatibility x effector compatibility interaction (F(1,11)=5.2, p=.044), indicating that the movement compatibility effect was greater in the effector compatible (52.9ms) than in the effector incompatible (18.2ms) condition. Simple effects analysis indicated a significant movement compatibility effect when the response effector was compatible with the stimulus effector (F(1,11) = 35.4, p<.0001, but only a trend in this direction when the response effector was incompatible (F(1,11) = 3.5, p=.088).

Thus, the results of the present experiment indicate that automatic imitation is not effector-independent. Opening and closing movements of an irrelevant action stimulus had more impact on the speed of opening and closing responses when the responses were performed with the modelled effector (hand responses to hand stimuli, and mouth responses to mouth stimuli) than when they were performed with the alternative effector (hand responses to mouth stimuli, and mouth responses to hand stimuli). Therefore, they imply that the effector-specificity of intentional imitation is not

entirely conventional; it is likely to reflect the operation of core imitation mechanisms, and not to be due solely to inferences about what is expected in the test situation.

However, the results of Experiment 5.1 did not distinguish clearly between the predictions of the generalist and specialist models of imitation. All three theories predicted the observed interaction between movement and effector compatibility, but whereas ASL and IM predicted that there would be an effect of movement compatibility in the effector incompatible condition, the AIM model predicted that movement compatibility would not influence performance in this condition. The results showed that movement compatible responses with the incompatible effector were substantially faster than movement incompatible responses with the incompatible effector, but this trend was not quite significant ($F(1,11) = 3.51$, $p=.088$).

Experiment 5.2

The principal purpose of Experiment 5.2 was to discriminate more decisively between the predictions of the generalist and specialist theories. Therefore, Experiment 5.2 replicated the basic design and procedure used in Experiment 5.1, but with an additional sample of participants. Experiment 5.2 had two further purposes: to check that the movement compatibility effect observed in Experiment 5.1 was not dependent on spatial compatibility, and to investigate the nature of the effector compatibility effects observed in Experiment 5.1.

In Experiment 5.1, hand stimuli moved in a horizontal plane (e.g. the fingers moved to the right of the screen when the hand opened), whereas hand and mouth responses were made in a vertical plane (e.g. the fingers and the upper lip moved upwards when participants made hand opening and mouth opening responses, respectively).

Therefore, in hand stimulus trials, the tendency to respond faster on movement compatible trials (e.g. hand or mouth opening in response to a hand open stimulus) could not have been due to spatial compatibility. However, in mouth stimulus trials, up-down spatial compatibility was confounded with movement compatibility. For example, in mouth open stimulus trials, the upper lip of the mouth stimulus moved upwards, and correct responses in the movement compatible condition involved upward movement of the participants' fingers or upper lip. To remove this confound, in Experiment 5.2 both the hand and the mouth stimuli moved in the horizontal plane. Thus, relative to Experiment 5.1, the mouth stimulus was rotated 90 degrees clockwise from the canonical position, so that the upper lip appeared on the right of the lower lip, and moved towards the right when the mouth stimulus opened. As in Experiment 5.1, responses were made when the participant's head was upright. If the movement compatibility effect observed in Experiment 5.1 was not dependent on up-down spatial compatibility, then it should be replicated in Experiment 5.2 where up-down spatial compatibility was controlled.

The third purpose of Experiment 5.2 was to investigate the effector compatibility effects found in Experiment 5.1. These effects showed that responses with the modelled effector (e.g. hand responses to hand stimuli) were faster, and more susceptible to automatic imitation, than responses with the alternative effector (e.g. hand responses to mouth stimuli). These effects might indicate that observation of an effector system in motion facilitates responding with an anatomically similar effector system, e.g. hand movement observation facilitates hand movements relative to mouth movements. However, these effects might indicate, instead or in addition, that observation of an effector system in motion facilitates responding at body-centred locations typically occupied by that effector system. For example, hand movement

observation may facilitate responses made in the typical locations of the hands (e.g. close to the middle of the trunk when seated) relative to responses made in the location of the mouth. To test the anatomical account against the response location account of effector compatibility, Experiment 5.2 varied the location of the response hand. In the 'far' condition, as in Experiment 5.1, the participant's responding hand rested on the desk top, just in front of their chest. In the 'near' condition, the participant's responding hand was located directly in front of their mouth. If the effector compatibility effects observed in Experiment 5.1 were due to the locations of the responding effectors, and not to the anatomical relationship between the stimulus and response effectors, then those effects should be substantially smaller in the near condition than in the far condition.

It is also possible, that the effector compatibility observed in Experiment 5.1 was related to the fact that participants could see their hand responses, albeit in peripheral vision, whereas they could not see their mouth responses. To control for this, in Experiment 5.2 a screen was placed between the participant's body and their responding hand, so that neither hand nor mouth responses were accompanied by visual feedback.

5.2.1 Method

Participants. Twelve additional participants, with an average age of 28.2 years (7 male) were recruited from the same source, and to meet the same requirements, as in Experiment 5.1.

Stimuli. The stimuli were identical to those in Experiment 5.1 except that the mouth stimuli were rotated by 90° in a clockwise direction from the canonical position, so

that the upper lip appeared on the right of the lower lip, and moved towards the right when the mouth stimulus opened (see Figure 15). As in Experiment 5.1, responses were made when the participant's head was upright. Therefore, for both hand and mouth stimuli, the stimulus movement (left/right) was orthogonal to the response movement (up/down).

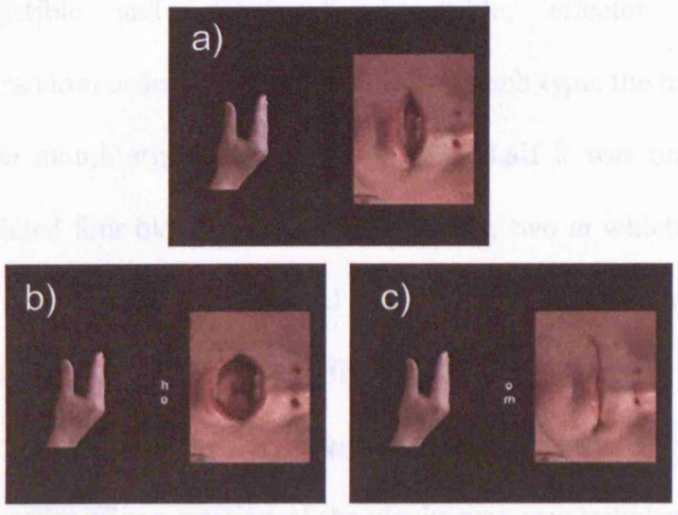


Figure 15: Experiment 5.2. Stimuli depicting a) the neutral warning stimulus, b) and c) two examples of imperative stimuli. In Figure 15b the irrelevant stimulus (open mouth) is effector compatible and movement incompatible with the required response (close mouth). In Figure 15c the irrelevant stimulus (close mouth) is effector incompatible and movement incompatible with the required response (open hand).

Procedure. The data recording and analysis were identical to Experiment 5.1. The procedure was also the same as in Experiment 5.1, except as follows. Participants completed eight blocks of trials over two sessions, between one and three days apart. Half of the blocks were completed in the 'hand far' position, where, as in Experiment 5.1, the hand was located approximately 400mm below the mouth. The remaining blocks were completed in the 'hand near' condition, where the participant's right arm lay in a horizontal position on a raised armrest such that the hand was as close as possible to the mouth in both the horizontal and vertical plane. In both conditions the hand was covered by a rigid black screen so that the participant could not see their

hand movements. Therefore, in Experiment 5.2, neither hand nor mouth responses yielded visual feedback.

Each block contained 64 trials in total, 16 trials of each of the four principal types (effector and movement compatible; effector compatible and movement incompatible; effector incompatible and movement compatible; effector and movement incompatible) in random order. In half of the trials of each type, the hand stimulus was on the left of the mouth stimulus, and in the other half it was on the right. Each participant completed four blocks of trials on each day, two in which the hand was in the near position and two in which the hand was in the far position. In one 'near' block the effector indicator (h or m) was above the movement indicator (o or c), and in the other near block it was below the movement indicator. This was also the case for the 'far' blocks. The order of presentation of the blocks was counterbalanced. Participants carried out the same four blocks on both days, but on the second day the order of near and far blocks was reversed.

5.2.2 Results and discussion

Practice trials, incorrect responses (2.9%) and response omissions (3.0%) were excluded from the analysis as were all RTs smaller than 100ms and greater than 1500ms (0.05%). The RT data for the 12 participants is shown in Figures 16 and 17.

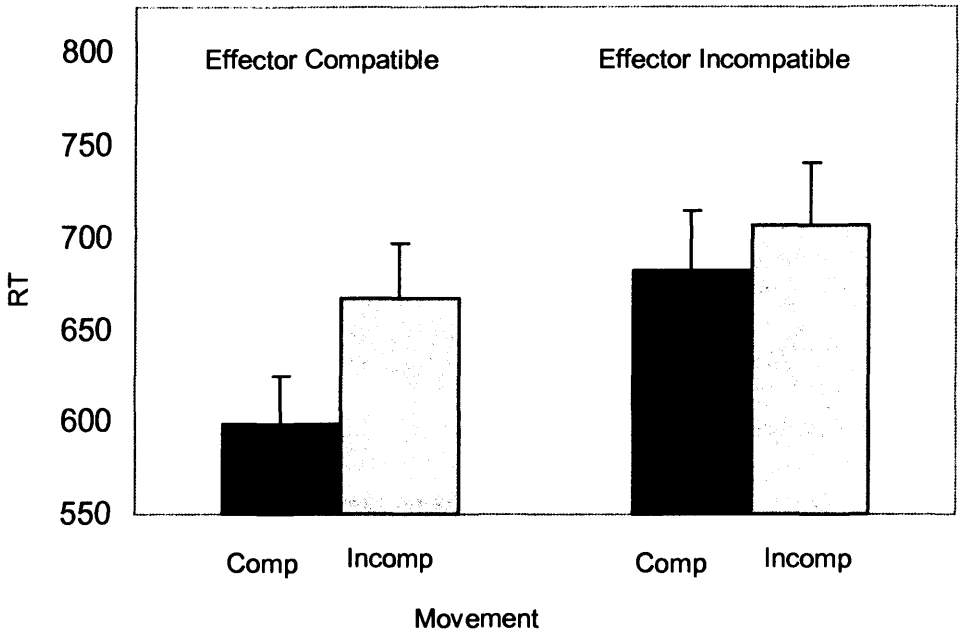


Figure 16: Experiment 5.2. Mean RT on movement compatible (black bars) and movement incompatible (grey bars) trials when effector is compatible (left side) and incompatible (right side). Vertical bars indicate the standard error of the mean.

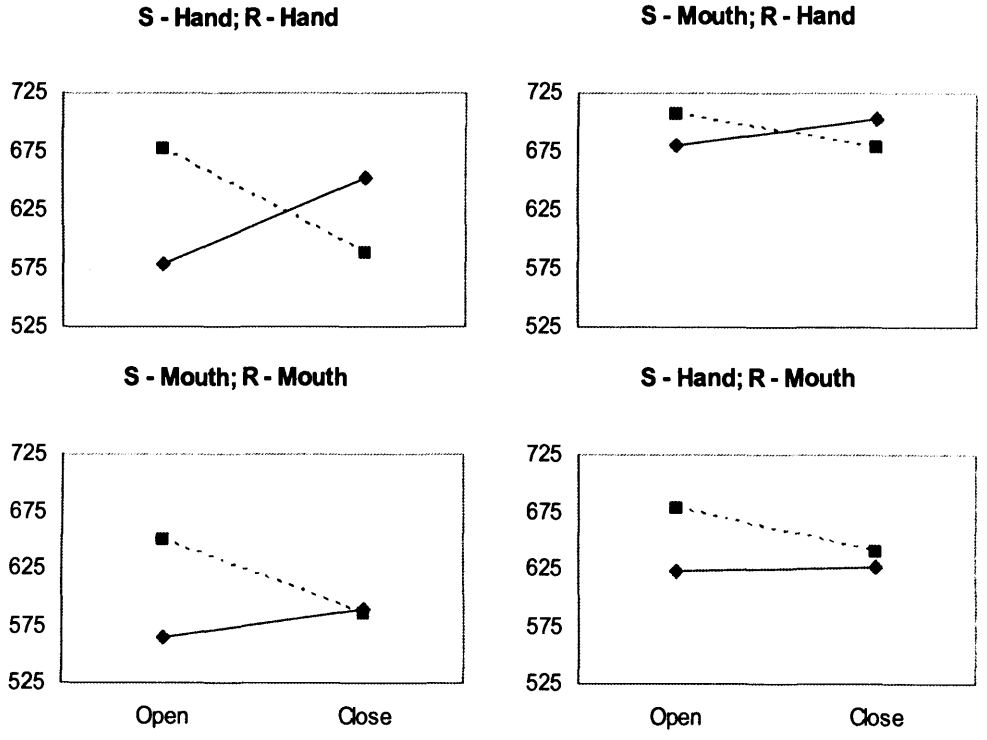


Figure 17: Experiment 5.2. Mean RT for open (diamonds and solid lines) and close (squares and dashed lines) movement responses for each trial type defined by the stimulus effector (S) and response effector (R) mapping.

The RT data were subjected to ANOVA in which movement compatibility (compatible and incompatible), effector compatibility (compatible and incompatible) response movement (open and close), response effector (mouth and hand) and hand position (near and far) were within-subjects variables. There were no significant main effects or interactions involving the hand position variable. There were significant main effects of movement compatibility ($F(1,11) = 58.4$ $p<.0001$), and effector compatibility ($F(1,11) = 39.0$, $p<.0001$). Participants were both faster to respond when the irrelevant stimulus movement was response compatible (Mean: 640.4 SEM: 28.4) than when it was response incompatible (Mean: 686.6 SEM 31.6), and when the irrelevant stimulus effector was response compatible (Mean: 633.2 SEM 26.9) than when it was response incompatible (Mean: 693.8 SEM 33.3). There were also significant main effects of response movement ($F(1,11) = 7.5$, $p=.02$) and of response effector ($F(1,11) = 12.4$, $p=.005$). Shorter RTs were recorded for mouth responses (Mean 644.3, SEM 30.2) than for hand responses (Mean 682.7, SEM 30.6), and for open responses (Mean 650.3, SEM 28.4) than for close responses (Mean 676.7, SEM 32.1).

The effect of movement compatibility was greater for closing than for opening responses (movement compatibility x response movement, ($F(1,11) = 11.4$, $p=.006$), but simple effects analysis confirmed that movement compatible responses were faster than movement incompatible responses both when the response was opening ($F(1,11) = 23.2$, $p=.001$), compatible: mean: 633.2; SEM: 27.6; incompatible: mean: 667.4 SEM: 29.5) and when it was closing ($F(1,11)=69.8$, $p<.0001$), compatible: mean: 647.6 ;SEM: 30.1 incompatible: mean: 705.9, SEM: 34.3). Similarly, the effect of effector compatibility was greater when responses were made with the hand than when they were made with the mouth (effector compatibility x response effector, $F(1,11) = 5.2$, $p=.04$), but effector compatible responses were faster both for mouth responses

($F(1,11) = 29.5$, $p<.0001$, compatible: mean: 619.9; SEM 28.0: incompatible: mean: 668.8 SEM: 32.9), and for hand responses ($F(1,11) = 32.8$, $p<.0001$, compatible: mean: 646.6; SEM 26.6: incompatible: mean: 718.3, SEM:35.2).

Of principal interest, there was a significant movement compatibility x effector compatibility interaction ($F(1,11) = 13.4$, $p=.004$), indicating that the movement compatibility effect was greater in the effector compatible (67.7ms) than in the effector incompatible (24.8ms) condition. Simple effects analysis indicated a significant movement compatibility effect when the response effector was compatible with the stimulus effector ($F(1,11) = 64.7$, $p<.0001$, and also when the response effector was incompatible with the stimulus effector ($F(1,11) = 8.7$, $p=.013$).

The results of the present experiment replicated and extended those of Experiment 5.1. Like Experiment 5.1, they showed that movement compatibility has less influence on performance when the stimulus and response effectors are incompatible than when they are compatible. Additionally, by controlling for any effects of up-down spatial compatibility on movement compatibility, Experiment 5.2 confirmed that the hand and mouth movement compatibility effects observed in these experiments were genuine; they were due to the relationship between the stimulus and response actions (opening and closing), and not simply to the elementary spatial properties of these actions. Similarly, by controlling for the possibility that, for example, hand movement stimuli prime movements at canonical hand locations, rather than hand movements *per se*, Experiment 5.2 confirmed that the effector compatibility effects observed in these experiments were due to the anatomical, rather that to the spatial, relationship between the stimulus and response effectors. Most importantly, the results of Experiment 5.2 confirmed that, although the effect of movement compatibility is smaller when the

stimulus and response effectors are incompatible than when they are compatible, the movement compatibility effect is significant in the effector incompatible condition. Thus, automatic imitation of movement trajectory occurs even when participants are responding with hand movement to mouth movement stimuli and vice versa. This finding, which was predicted by IM and the ASL model, suggests that the core mechanisms of imitation operate in a way that is partially, but not wholly, effector-specific.

5.3 General discussion

In everyday life, and in laboratory tasks where participants intend to imitate, movements are usually imitated with the modelled effector system, e.g. hand movements are imitated with the hands and foot movements with the feet. To investigate whether this effector-specific tendency in intentional imitative performance reflects the nature of the core mechanisms of imitation, a SRC paradigm was used to investigate the effector-specificity of automatic imitation. The results of two experiments indicated an automatic imitation, or movement compatibility, effect both when participants responded with the modelled effector system (effector compatible condition) and when they responded with an alternative effector system (effector incompatible condition), and that the movement compatibility effect was smaller when an alternative effector was used. More specifically, opening and closing movements of an irrelevant action stimulus had more impact on the speed of opening and closing responses when the responses were performed with the modelled effector (hand responses to hand stimuli, and mouth responses to mouth stimuli) than when they were performed with the alternative effector (hand responses to mouth stimuli, and mouth responses to mouth stimuli).

Previous studies have demonstrated movement compatibility effects for hand opening and closing stimuli when the stimulus and response effectors were compatible (Heyes et al., 2005; Press et al., 2005; Stürmer et al., 2000), but the experiments in this chapter show for the first time 1) that opening and closing mouth movements are susceptible to automatic imitation, 2) that automatic imitation of opening and closing movements of the hand and mouth transfers across these effector systems, and 3) that the transfer is incomplete; automatic imitation of opening and closing movements of the hand and mouth is partially effector-specific.

As its name suggests, automatic imitation is likely to be less susceptible to cognitive control than imitative performance based on instructions or when a participant intends to carry out an imitative act (Press et al., 2006). Therefore, any effector-specificity observed in an automatic imitation task is unlikely to be due to the participant inferring that they should match both effector and movement. Therefore, the effector-specificity of automatic imitation observed in the present study suggests that, in intentional imitation tasks and in everyday life, participants do not imitate with the modelled effector purely because they judge effector matching to be conventional. Rather, it suggests that the effector-specificity of imitative performance reflects the structure of the core mechanisms of imitation; the mechanisms that solve the correspondence problem (Brass & Heyes, 2005) by translating visual input from observed body movements into matching motor output.

The active intermodal matching theory (AIM, Meltzoff & Moore, 1997) suggests that the mechanisms that solve the correspondence problem operate in two stages. The first stage identifies the modelled effector, and, when it is completed, the second stage codes the movement performed by that effector. This account implies that the

mechanism mediating movement imitation, operative in the second stage, is strictly effector-specific; that it represents the modelled movement in codes that apply exclusively to the modelled effector. If this is correct, then the AIM model is not consistent with the results of the present study, which indicated only partial effector-specificity of automatic imitation.

In contrast, the findings of the present study are consistent with both the ASL model of imitation (Heyes & Ray, 2000; Heyes 2001) and IM (Prinz, 1997; 2002). ASL suggests that visual input from the model is translated into motor output by a set of bidirectional, excitatory links connecting visual and motor representations of the same action components. These 'vertical associations' are thought to be established through associative learning; formed on the basis of correlated experience of observing and executing action components. Because stimulus generalization is a ubiquitous feature of associative learning (Pearce, 1994), the ASL model assumes that vertical associations are activated, not only by the stimuli experienced during learning, but also by other stimuli to the extent that they have physical characteristics in common with the learned stimulus (Press et al., 2005; 2006). Similarly, IM proposes a role for visual similarity, suggesting that observation of a perceptual stimulus activates the action representation with which it exhibits the most similarity. Therefore, both generalist theories would make the same prediction regarding the partial effector-specificity of the mechanisms of imitation. More specifically, these theories would expect some facilitation of mouth opening by observation of hand opening, and vice versa, given the visual similarity between the opening movement of a mouth and the opening movement of a hand. Consistent with this prediction, the results of Experiments 5.1 and 5.2 indicated partial effector-specificity - a smaller but significant movement compatibility effect when the stimulus and response effectors were incompatible.

While the present findings illustrate the congruence between the two generalist theories addressed in this thesis, they also highlight one difference between these theories. IM can readily explain automatic imitation of hand movements because they are perceptually transparent, i.e. they yield similar visual effects when observed and executed. Automatic imitation of mouth movements, which was demonstrated in adult participants for the first time in these experiments, is harder to reconcile with IM. This is because mouth movements are perceptually opaque; they yield dissimilar sensory input when observed and executed. For example, when I open my mouth I do not receive any distinctive visual input, but when I observe someone else opening their mouth, I see the lips parting and forming an oval shape. However, IM is able to explain imitation of perceptually opaque actions, and partial effector-specificity of automatic imitation, when it is combined with the hypothesis, central to the ASL model, that actions acquire their 'common', sensory codes through associative learning (Elsner & Hommel, 2001; 2004). Associative learning allows perceptually opaque actions to be represented by sensory effects which are dissimilar to the direct effects of action execution, but which have been reliably correlated with action execution. For example, although the sight of an opening mouth is not a direct and anatomically inevitable consequence of my opening my mouth, I may learn to represent my mouth opening movement from a third party perspective as a result of being imitated, or looking in a mirror, while performing this action (Heyes & Ray, 2000). Experiences of this kind establish the third party perspective as part of the representation of the executed action, and thereby allow IM to invoke the principle of similarity to explain both automatic imitation of perceptually opaque actions, and the partial effector dependence observed in the present experiments.

In conclusion: The results of the present study indicate that automatic imitation is partially effector-specific: observation of opening and closing movements of the hand and mouth prime execution of corresponding movements by the modelled effector and also by the alternative effector, but the priming effect is smaller when the alternative effector is engaged in responding. This finding suggests that, rather than being conventional, the effector-specificity of intentional imitation reflects the nature of the mechanisms that mediate visuomotor translation for imitation. The partial effector-specificity observed in this chapter is consistent with the ASL and IM theories of imitation, and not consistent with the AIM model. This chapter, therefore, provides positive support for generalist theories of imitation.

Chapter 6: Discussion

6.1 Overview

This chapter summarises the findings from the previous chapters with reference to the theoretical questions they addressed. The findings in each chapter will be outlined, along with likely interpretations of those findings. Following these summaries, implications and limitations of the experiments will be discussed along with outstanding questions. Section 6.2 reviews Chapter 2, which investigated the role of goals in imitation. Section 6.3 discusses Chapters 3 and 4 which examined imitation skills in ASD, and section 6.4 reviews Chapter 5 which examined effector-specificity in imitation. Finally, section 6.5 considers the implications of this whole body of experimental work and presents general conclusions.

6.2 Intentional imitation in typically developing individuals

6.2.1 Summary and interpretation

The purpose of this thesis was to investigate how the correspondence problem is solved, and thus, how we are able to imitate. The two specialist theories under consideration suggest that imitation is mediated by a special-purpose mechanism whereas the two generalist theories suggest that imitation is mediated by general learning and motor control mechanisms.

Both of the specialist theories highlight the role of goals in explaining how we imitate. The goal-directed theory of imitation (GOADI) provides the most explicit statement of this view. Some evidence in favour of this theory has been provided by the well-replicated finding that, when they are required to imitate, children and adults more

accurately reproduce the goal of the action than the means used to carry out that action. For example, in the pen-and-cups task, participants imitate object selection more accurately than effector selection, which is imitated more accurately then grip selection.

However, an alternative explanation of these findings has been provided by a 'general process account', which suggests that task-general processes, of perception and attention, can explain the types of imitative behaviour that are commonly thought to support a goal-directed view. According to this account, goals are not necessary to explain the findings from imitation tasks such as the pen-and-cups task.

Some evidence in favour of the general process account was provided by Bird et al. (in press) who demonstrated that when the colour cue was moved from the cups to the hands or the grips, these components became the most accurately imitated components of the action, thus demonstrating a colour minimum error pattern. However, the results from this study only undermine the claim that goals guide performance on this task if one assumes that goals are action end-states. On the contrary, the mentalistic version of GOADI (mGOADI) claims that goals are inferred mental states of the model. This interpretation of the GOADI model is compatible with the results of Bird et al. because it is possible that the colour cue in these experiments affected imitative performance by changing the action component inferred by the participant to be the goal of the movement.

Therefore, Experiments 2.1 and 2.2 tested mGOADI against a general process account using the pen-and-cups task. In Experiment 2.1, participants were either required to respond to naturalistic or moving geometric stimuli. Geometric stimuli are unlikely to

support the attribution of mental states and yet the colour minimum error pattern was observed in both versions of this task. This result is consistent with the general process account but inconsistent with mGOADI. In Experiment 2.2 static geometric shapes were used to reduce further the possibility that participants attributed intentions to the shapes. Furthermore, in this task, participants either carried out movements or responded verbally. The colour minimum error pattern was observed in both tasks providing further evidence consistent with a general process account and inconsistent with mGOADI.

In the geometric version of the task, where mental state attribution is unlikely, it is highly probable that error patterns arise from general perceptual and attentional processes. Given that the same error patterns were observed in both geometric and naturalistic versions of the task, it is likely that error patterns in the naturalistic version of the task also arise from general processes. Thus, the findings from this chapter suggest that mentalistic goals are not necessary to explain the colour minimum error pattern. Rather, general processes, which mediate performance in a range of tasks, can account for the error patterns seen in the pen-and-cups task. Consequently, error patterns, such as those demonstrated in this task, cannot be used as evidence for goal directed accounts.

Therefore, the findings from Chapter 2 challenge one line of evidence that has been put forward to support specialist theories of imitation. Furthermore, in demonstrating that task-general processes can explain imitation errors, the present findings are consistent with generalist theories of imitation which suppose that there are no imitation-specific processes.

6.2.2 Limitations and outstanding questions

The principle finding of this chapter was similar error patterns in geometric and naturalistic versions of the pen-and-cups task. On the basis of this finding, I have concluded that performance on the naturalistic task does not rely on the attribution of intentions. However, it is possible that different processes guide performance in the naturalistic version and in the geometric version, and that these processes happen to result in similar error patterns. More specifically, when imitating human action stimuli, one may be guided by inferences about the intentions of the model, but when reacting to abstract geometric shapes, one may be guided by more general perceptual and attentional processes.

This explanation for the results of Experiments 2.1 and 2.2 is unparsimonious, but it cannot be ruled out with reference to these data alone. However, some findings from Chapter 3 suggest that this alternative explanation is unlikely to account for the current findings. Chapter 3 provided further evidence that is inconsistent with the view that performance on the pen-and-cups task is guided by inferences about intentions. In Experiment 3.1, individuals with ASD carried out the naturalistic version of the pen-and-cups task. These individuals have well-documented difficulties in inferring the intentions of others (e.g. Frith & Frith 2003). Therefore, if performance on this task relies on such a skill, we may expect to see different error patterns in these individuals compared with controls. Contrary to this prediction, in Experiment 3.1, individuals with ASD showed the typical cup<hand<grip error pattern, providing further evidence that intention reading is not involved in this task.

Chapter 2 highlights the role of general processes rather than goals in imitation but it does not identify the exact nature of the general processes that generate the colour

minimum error pattern. It has been suggested by Bird et al. (2007) that these general processes are perceptual and attentional. In Experiments 2.1 and 2.2, a stimulus variable, colour, modulated accuracy of performance. Thus, the colour cue could have improved performance in several ways. For example, differential colouring of the two levels of an action variable (cup, hand or grip) could have enhanced their discriminability directly, making it easier to see on each trial which variant had been selected by the model. Alternatively, colouring of an action variable may draw a participant's attention to a particular component resulting in that component being the focus of spatial attention. Further investigation may shed light on exactly which processes influence performance. However, the failure to identify exactly which general processes have the greatest influence on performance does not detract from the principle message of this chapter. The processes mentioned above are task-general. Perceptual discrimination and attentional selection occur in a range of perceptual-motor tasks, not just in those requiring imitation. Therefore, whatever range and combination of these processes was responsible for the effects observed in the present experiments, the present results support the view that general mechanisms, rather than imitation-specific processes of goal-selection, explain imitation errors.

The findings from Chapter 2 challenge one set of results that have been suggested to support GOADI. Other similar results using different paradigms have also been suggested to support GOADI. For example, the authors of GOADI have said that contralateral-to-ipsilateral error patterns observed in the dots and hand-to-ear tasks demonstrate goal-directedness in imitation (e.g. Bekkering et al., 2002). Like the error patterns in the pen-and-cups task, it is possible that these results may also be explained with reference to a general process account. It is plausible that, in the hand-to-ear and dots tasks, contralateral-to-ipsilateral errors are common because, during the trials in

which they occur, the locations of the two objects (ears or dots) are fixed, whereas the locations of the two effectors (hands or fingers) change in the course of the trial (e.g. from left to right hemispace and back again). Consequently, effector selection is likely to be harder to discriminate than object selection, and therefore trials in which object selection is correct and effector selection incorrect (contralateral-to-ipsilateral errors) will occur more frequently than, for example, trials in which effector selection is correct and object selection incorrect (ipsilateral-to-contralateral errors). Appropriate experiments would be necessary to verify these predictions, but given the findings from Chapter 2, it is likely that error patterns in paradigms, like the dots and hand-to-ear tasks, can also be explained by general processes.

The findings from Chapter 2 have implications for research which uses performance on imitation paradigms as an indicator of theory of mind skills. For example, Want and Gattis (2005) argued that children with impaired theory of mind should also demonstrate impaired goal-directed imitation, that is, they should not show the typical error patterns on the dots task. They tested the imitative abilities of late-signing deaf children with suspected theory of mind impairments and found their performance to be equivalent to control children. This finding prompted Want and Gattis to conclude that late-signing deaf children had inferred the goals of the demonstrator, and therefore that an early form of mental state understanding was intact in these children. In opposition to this view, the results of Chapter 2 suggest that an understanding of mental state goals is not necessary to explain performance in some imitation tasks. Thus, conclusions about theory of mind ability based on tests of imitative performance may be unwise.

6.3 Imitation in ASD

6.3.1 Summary and interpretation

Chapters 3 and 4 investigated imitative abilities in ASD. Whether or not an imitation impairment exists in ASD is relevant to the topics discussed in this thesis. Special-purpose mechanisms should be susceptible to selective impairment. That is, an impairment in one task domain that is not associated with more generalised deficits in other task domains. Therefore, compelling evidence of a selective imitation impairment in ASD may provide support for specialist theories of imitation.

Although the majority of studies have reported impaired imitation performance among individuals with ASD, there have been some conflicting findings, with some studies failing to show impairments. One source of the variance in imitation performance across studies may be the type of tasks used to measure imitation. The majority of tasks used to date have been complex intentional imitation tasks requiring a number of abilities in addition to imitation which may influence performance on these tasks.

Chapters 3 and 4 examined two possible explanations for the mixed findings in the ASD imitation literature. First, there is a genuine imitation-specific impairment in ASD. Second, there is no specific imitative impairment in ASD; rather, poor performance on tests of imitation is due to impairments of non-specific abilities which are required for successful performance on these tests. Chapters 3 and 4 aimed to distinguish between these possibilities by examining imitation performance in an intentional (Chapter 3) and an automatic imitation (Chapter 4) paradigm.

6.3.1.1 Intentional imitation in individuals with ASD

The majority of studies demonstrating impaired performance on imitation tasks have used complex intentional imitation paradigms. Chapter 3 sought to replicate one such finding of impaired performance and to investigate the source of this impairment. Employing the pen-and-cups task, Experiment 3.1 replicated previous findings of impaired performance on an intentional imitation task. Experiment 3.2 investigated the source of this poor performance using non-imitative versions of the pen-and-cups task. In Experiment 3.2, one task involved action responses being made to abstract geometric stimuli, while the other required participants to describe the original action stimuli. If the poor performance on the imitative version of the task was due to an imitation-specific impairment, one would expect improved performance when the task is changed so that it presents equally challenging general task demands but is non-imitative. However, contrary to this prediction, the ASD group was as impaired, relative to the control group, on each of the non-imitative versions of the pen-and-cups task. This pattern of results is inconsistent with claims of an imitation-specific impairment in ASD. Rather it suggests that, at least in the pen-and-cups task, the observed imitation impairment can be fully explained by processes that are not specific to imitation.

6.3.1.2 Automatic imitation in individuals with ASD

The results from Chapter 3 suggested that impaired imitation performance in individuals with ASD could be explained by processes not specific to imitation. These processes are necessary for carrying out complex intentional imitation tasks such as the pen-and-cups task. In order to minimise demands made on non-specific processes, a simple automatic imitation paradigm was used. If, as the results from Chapter 3

suggest, poor performance on imitation tasks results from impairments in non-imitation-specific processes, we should not expect poor performance in an imitation task where demands on these non-specific processes are minimised.

In Experiment 4.1, participants were required to make a pre-specified response (open or close hand) to an open or closed hand on the screen. The stimuli were either human or robotic hands and the movement of the hand stimulus was either the same as, or the opposite of, the pre-specified response. The principal finding of this experiment was that individuals with ASD showed intact automatic imitation. This was demonstrated both by a compatibility effect and an animacy bias comparable to the effects observed in controls. By reducing non-specific task demands, the results from this chapter provided evidence suggesting that individuals with ASD do not have an imitation-specific impairment.

6.3.2 Limitations and outstanding questions

In Experiment 3.1, the ASD group made more errors than controls in the imitative version of the pen-and-cups task, whereas Experiment 4.1 demonstrated intact performance on an automatic imitation task. Accordingly, it could be argued that Chapters 3 and 4 have demonstrated impaired intentional imitation and intact automatic imitation. As a result, it could be claimed that individuals with ASD have a specific impairment in intentional imitation with spared automatic imitation capabilities. This may imply a selective imitation impairment in ASD which is more consistent with a specialist than with a generalist view of imitation. However, there are a number of reasons to doubt this interpretation.

First, McIntosh et al. (2006) investigated intentional and automatic imitation of facial movements in individuals with ASD. In this study, the opposite pattern was demonstrated, whereby individuals with ASD showed impaired automatic and intact intentional imitation.

Second, there is no reason to suppose that the core mechanisms that mediate intentional imitation differ from those that mediate automatic imitation. In both automatic and intentional imitation, one is required to translate a visual representation from observing an action into the motor output necessary to execute that action. In addition, there is some evidence that both intentional and automatic imitation rely on the same cortical areas. That is, similar cortical activation is observed both when observing and executing action and when intentionally imitating (Rumiati, Weiss, Tessari, Assmus, Zilles, Herzog, & Fink 2005; Iacoboni et al., 1999). Therefore, it appears that both intentional and automatic imitation rely on the same psychological and neurological mechanism. Consequently, it is difficult to conceive of an impairment in an imitation-specific process that affects intentional but not automatic imitation.

The crucial difference between intentional imitation and automatic imitation is the intention or will to imitate. Therefore, if individuals with ASD show particularly poor performance on tasks of intentional imitation, it is likely that it is this intention to imitate that is atypical. That is, individuals with ASD are not as motivated to imitate as are typically developing individuals. This idea is consistent with the message of Chapters 3 and 4. An abnormal intention to imitate would not constitute an imitation-specific impairment as motivation to imitate is likely to be part of a larger impairment in social interaction.

Experiments 3.1, 3.2 and 4.1 examined imitation performance in an ASD sample of adults with above average IQ. It could be argued that a specific impairment would have been detected if children or individuals with lower IQ had been tested. While it is possible that different populations within the autism spectrum may show an alternative pattern of results, this possibility may not undermine the conclusions drawn in this thesis.

First, if imitation impairments were observed in individuals with lower IQ then this would not constitute a selective imitation impairment in ASD, since imitation impairments would co-exist with generalised deficits. Impairments in a particular domain only constitute support for specialist claims if those impairments are selective (e.g. Gopnik 1990; Leslie, 1992; Karmiloff-Smith, 2000). More specifically, any imitation impairments in individuals with low IQ could result from generalised cognitive impairments rather than a specific imitation deficit. Consequently, such a pattern of results would not be able to provide support for specialist theories.

Second, if imitation impairments were observed in children with ASD, this would indicate that imitation impairments in ASD are delayed rather than deviant. Consistent views have been presented by Whiten & Brown (1999) and by Williams et al. (2004). If development of a particular skill is delayed, this implies an important role for learning and environmental input, which is consistent with generalist theories and not specialist views of imitation. In particular ASL, which highlights the role of learning in imitation, may expect some delayed development of imitative ability in individuals with ASD. If as ASL suggests, the sensorimotor links necessary for imitation are formed through experience, young children with ASD may show impaired performance. Since they spend less time attending to social stimuli, children with ASD

may have been exposed to fewer social situations in which they could gain concurrent experience of seeing and doing. One may expect especially poor imitation skills for opaque actions such as facial expressions and whole body movements since the relevant experience needed to learn how to imitate these actions cannot be gained through self observation. If individuals with ASD prefer not to look at others they may not have gained enough relevant experience to learn associations between visual and motor representations of opaque actions. Therefore, further investigation into the source of imitative abilities in younger individuals with ASD is necessary and this investigation should focus on imitative abilities both in opaque and transparent actions.

Although delayed development of imitation skills implies an important role for learning, it is not wholly inconsistent with a specialist view of imitation. It is plausible that a specialised imitation mechanism is only 'switched on' later in development in ASD resulting in delayed acquisition of imitation skills (Baron-Cohen, 1992). Therefore, in order to clarify this matter, it is necessary to carry out further studies with children with ASD. These studies should aim to minimise task demands, like Experiment 4.1, in order to ascertain whether any observed imitation impairments in children arise from a specific imitation impairment or from impairments in more general processes.

The findings from this thesis suggest that there is no imitation-specific impairment in ASD but they do not lend support to any particular theory regarding the core deficit in ASD. There are a number of candidate impairments that would be consistent with the findings in this thesis.

For example, individuals with ASD may have abnormalities in the perception of dynamic stimuli (e.g. Milne, Swettenham, Hansen, Campbell, Jeffries & Plaisted, 2002). All of the stimuli used in Chapter 3 were complex dynamic stimuli, and therefore difficulty in perceiving such stimuli could have resulted in impaired performance on these tasks. Alternatively, impairments in motor planning or motor control may explain some of the poor performance. However, this would not explain why poor performance was also observed on the verbal task in Chapter 3, because demands placed on motor control and planning were reduced in this task. Furthermore, attentional impairments may explain some of the poor performance observed in Chapter 3. More specifically, individuals may have impairments in the rapid shifting of attention between the three action components inherent in all versions of the pen-and-cups task. Many studies have detailed attentional impairments in ASD; examples include prioritizing dynamic stimuli (Greenaway & Plaisted, 2005), allocating attention in the presence of distracters (Burack, 1994), and switching the attentional focus rapidly between spatial locations (Wainwright & Bryson, 1996; Landry & Bryson, 2004), and object features (Courchesne, Townsend, Akshoomoff, Saitoh, Yeung-Corchesne, Lincoln, James, Haas, Schreibman & Lau, 1994). However, it is not within the scope of this thesis to pin down the exact nature of impairments in ASD and further exploration of candidate abilities is necessary.

6.4 Automatic imitation in typically developing individuals

6.4.1 Summary and interpretation

The final empirical chapter examined effector-specificity in imitation. In everyday life, when we intend to imitate, movements are usually imitated with the modelled effector system, e.g. we imitate hand movements with our hands and foot movements with our

feet. To investigate whether this effector-specific tendency in imitative performance reflects the nature of the core mechanisms of imitation, a SRC paradigm was used to investigate the effector-specificity of automatic imitation, and thereby the specialist or generalist nature of the core mechanisms of imitation.

Experiments 5.1 and 5.2 indicated an automatic imitation, or movement compatibility, effect both when participants responded with the modelled effector system (effector compatible condition) and when they responded with an alternative effector system (effector incompatible condition), and that the movement compatibility effect was smaller when an alternative effector was used.

The findings from this chapter are inconsistent with the claims made by AIM, which would predict complete effector-specificity in this task. AIM supposes that the mechanisms that solve the correspondence problem operate in two stages. The first stage identifies the modelled effector, and, when it is completed, the second stage codes the movement performed by that effector. This account implies that the mechanism mediating movement imitation, operative in the second stage, is strictly effector-specific; that it represents the modelled movement in codes that apply exclusively to the modelled effector.

The findings in this chapter were consistent with ASL and IM which both predict partial effector specificity in this task. ASL suggests that visual input received from observing action is translated into motor output by a set of bidirectional, excitatory links connecting visual and motor representations of the same action components. These 'vertical associations' are thought to be established through associative learning; formed on the basis of correlated experience of observing and executing action

components. Because stimulus generalization is a ubiquitous feature of associative learning (Pearce, 1994), the ASL model assumes that vertical associations are activated, not only by the stimuli experienced during learning, but also by other stimuli to the extent that they have physical characteristics in common with the learned stimulus (Press et al., 2005; 2006).

Similarly, IM suggests that actions are represented in terms of their sensory consequences, and that action observation primes performance of an action to the extent that the observed and executed actions have similar sensory consequences. Therefore, the observation of a hand opening will be most likely to prime performance of a hand opening response as the sensory consequences of these two events are most similar. However, since the sensory consequences of mouth opening and hand opening have features in common, observation of a hand opening action may prime a mouth opening response, but to a lesser extent than it primes a hand opening response.

Therefore, in demonstrating partial effector-specificity, the results from this chapter provide support for generalist theories of imitation.

6.4.2 Limitations and outstanding questions

The findings from Chapter 5 have been suggested to support generalist, rather than specialist theories of imitation. However, it could be argued, in line with the specialist theories examined in this thesis, that the reason why automatic imitation effects were observed even when the effector was incompatible was because the actions were coded in terms of their goal. For example, one might be quicker to open one's hand in response to an open mouth than to a closed mouth because one codes the observed

action in terms of its outcome, in this case 'open'. However, if, as this interpretation suggests, we code actions exclusively in terms of their outcomes, then we should not expect any effect of effector; there should be no effector-specificity in this task. Contrary to this predication, significant effector compatibility effects were found in Experiments 5.1 and 5.2.

Alternatively, it could be argued that the results of Experiments 5.1 and 5.2 do not arise from relationships between the irrelevant stimuli and the responses (stimulus-response or S-R compatibility) but rather from the relationships between the irrelevant stimuli and the imperative stimuli (stimulus-stimulus or S-S compatibility). For example, when one sees a hand moving one may be faster to process the 'h' stimulus than the 'm' stimulus, or vice versa. If this is the case then the result of experiments 5.1 and 5.2 have little to do with imitation because imitation requires a translation of a visual stimulus into a motor response. S-S relationships arise from the processing of one visual stimulus interfering with the processing of another visual stimulus. Effects that are solely due to S-S relationships therefore cannot provide evidence that is directly relevant to theories of imitation that address the correspondence problem.

The S-S compatibility interpretation cannot be ruled out on the basis of the results of Experiments 5.1 and 5.2 alone. However, it is implausible for a number of reasons.

First, in previous SRC procedures used to examine automatic imitation, similar compatibility effects have been obtained both when simple RT and choice RT paradigms were used (e.g. Press et al., 2006). Whereas in choice RT paradigms compatibility effects may arise from S-S or from S-R relationships, in simple RT paradigms there is only one stimulus type (imperative stimulus) present. Therefore,

effects observed in simple RT paradigms must be due to the relationship between the stimulus and the response.

Second, the procedure used in Experiments 5.1 and 5.2 can be formally described as a Simon SRC task or, according Kornblum's taxonomy, a Type-3 ensemble (Kornblum 1992; 1994). Many studies have revealed parallels between SRC effects in experiments with body movements, that are used to study imitation, and SRC experiments with arbitrary stimuli in the general SRC literature (e.g. Heyes & Ray, 2004). Therefore, it is reasonable to expect that the principles established using arbitrary stimuli and Simon tasks in the general SRC literature will also apply to experiments, like 5.1 and 5.2, that use similar procedures to study imitation. The general SRC literature suggests that the compatibility effects that occur in Simon tasks are due primarily to S-R, rather than S-S relationships (e.g. Hommel, 1993; 1995; 1997; Kornblum, Hasbroucq & Osman, 1990; Lu & Proctor, 1995). For example, Simon effects are observed even when there is no consistent relationship between the imperative stimulus and the irrelevant stimulus dimensions (Hommel, 1995). Therefore, it is likely that in the SRC tasks used to investigate imitation, such as those in Experiments 5.1 and 5.2, any compatibility effects are also due to the S-R relationships.

In addition to demonstrating the effector specificity of automatic imitation for the first time, Chapter 5 also constitutes the first demonstration of automatic imitation of opaque actions. Some previous studies have shown automatic imitation of facial expressions but in these studies emotional stimuli were used (e.g. Dimberg, Thunberg & Elmehed, 2000; Platek, Mohamed & Gallup, 2005). Therefore, it is not clear whether the effects demonstrated in these previous studies were genuinely automatic imitation effects, or instead whether they resulted from emotional contagion. In

Chapter 5, mouth opening and closing stimuli were used which are less likely to be associated with emotions than the stimuli used in previous studies. Thus, the present results demonstrate that even for perceptually opaque actions, where the correspondence problem is most challenging, action observation automatically leads to motor activation.

6.5 Conclusions

The experiments described in this thesis have used a number of new experimental methods to generate novel findings with respect to automatic and intentional imitation. First, this research has used a novel geometric variant of the pen-and cups task to show that mentalistic goals are not an intrinsic part of the core mechanisms of imitation. Second, this novel task has been used to provide evidence which suggests that there is no imitation-specific impairment in ASD. Third, this research has demonstrated intact automatic imitation in individuals with ASD for the first time. Finally, automatic imitation of opaque actions and partial effector-specificity of automatic imitation has been demonstrated for the first time.

Furthermore, the collective results from these experiments have allowed me to address the central issue discussed in this thesis, that is, *how* we are able to imitate. Successful imitation requires translation of a visual representation into a matching motor output. A number of theories have been suggested to explain how this correspondence problem may be solved. These theories are either specialist or generalist theories. The principle aim of this thesis was to discover whether specialist or generalist theories can best explain how we are able to imitate.

Chapters 2, 3 and 4 examined two lines of evidence that have been suggested to support specialist theories of imitation, the role of goals in imitation and the existence of a selective imitation impairment ASD. The results from the experiments presented in these chapters have challenged this evidence. These findings imply that neither line of evidence can be used to support specialist claims. Finally, Chapter 5 provided some specific support for both generalist theories addressed in this thesis.

Therefore, the results presented in this thesis are more consistent with a generalist view of imitation. From the present experiments, there appears to be little compelling evidence of a special-purpose mechanism dedicated to imitation. Instead, the data presented here support the generalist view that imitation is mediated by general learning and motor control mechanisms.

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